IMPACTS OF A TOP PREDATOR (*ESOX LUCIUS*) ON SALMONIDS IN SOUTHCENTRAL ALASKA: GENETICS, CONNECTIVITY, AND VULNERABILITY

By

Chase S. Jalbert, B.S.

A Thesis Submitted in Partial Fulfillment of the Requirements

for the Degree of

Master of Science

in

Fisheries

University of Alaska Fairbanks

December 2018

APPROVED:

Dr. Jeffrey Falke, Committee Co-Chair
Dr. Peter Westley, Committee Co-Chair
Dr. J. Andrés López, Committee Member
Mrs. Kristine Dunker, Committee Member
Dr. Milo Adkison, Chair
Department of Fisheries
Dr. S. Bradley Moran, Dean
College of Fisheries and Ocean Sciences
Dr. Michael Castellini, *Dean of the Graduate School*

Abstract

Worldwide invasion and range expansion of northern pike (pike; *Esox lucius*) have been linked to the decline of native fishes and new techniques are needed to assess the effects of invasion over broad geographic scales. In Alaska, pike are native north and west of the Alaska Mountain Range but were introduced into Southcentral Alaska in the 1950s and again in the 1970s. To investigate the history of the invasion into Southcentral Alaska, I identified 7,889 single nucleotide polymorphisms (SNPs) from three native and seven introduced populations in Alaska and examined genetic diversity, structure, and affinities of native and invasive pike. Pike exhibited low genetic variability in native populations (mean heterozygosity = 0.0360 and mean $\pi = 0.000241$) and further reductions in introduced populations (mean heterozygosity = 0.0227 and mean $\pi = 0.000131$), which suggests a bottleneck following introduction. Population differentiation was high among some populations (global $F_{ST} = 0.424$; max $F_{ST} = 0.668$) when compared to other freshwater fishes. I identified five genetically distinct clusters of populations, consisting of three native groups, a single Susitna River basin invasive group, and a Kenai Peninsula group, with little evidence of admixture among groups. The extremely reduced genetic diversity observed in invasive northern pike populations does not appear to affect their invasion success as the species range Southcentral Alaska continues to expand. To assess the vulnerability of five species of Pacific salmon (*Oncorhynchus* spp.) to the invasion, I combined intrinsic potential habitat modeling, connectivity estimates, and Bayesian networks across 22,875km of stream reaches in the Matanuska-Susitna basin, Alaska, USA. Pink salmon were the most vulnerable species, with 15.2% (2,458 km) of their range identified as "highly" vulnerable. They were followed closely by chum salmon (14.8%) and coho salmon (14.7%). Finally, analysis of the intersection of vulnerable salmon habitats revealed 1,001 km of streams that were highly

vulnerable for all five Pacific salmon. This framework is easy to implement, adaptable to any species or region, and cost effective. With increasing threats of species introductions, fishery managers need new tools like those described here to efficiently identify critical areas shared by multiple species, where management actions can have the greatest impact.

Table of Contents

Page

THIS PAGE INTENTIONALLY LEFT BLANK

List of Figures

Page

List of Tables

Page

THIS PAGE INTENTIONALLY LEFT BLANK

List of Appendices

Page

Acknowledgments

First, I would like to thank my advisors and wordsmiths Dr. Jeffrey Falke and Dr. Peter Westley for their support, motivation, and mentorship throughout this project. The tremendous insight, input, and expertise from my committee members, Dr. Andres Lopez and Mrs. Kristine Dunker was invaluable to this project. This project would not have been possible without the support of Dr. Adam Sepulveda of the United States Geological Survey Northern Rocky Mountain Science Center who provided funding, insight, and helped with sampling. Also, I'm appreciative to the Alaska Department of Fish and Game, specifically the Sport Fish graduate program and agency staff from across the state who have helped shape my career and put me on the path to graduate school. I would like to thank the lab technicians from the University of Alaska Museum Fish Genetics lab, who spent many hours extracting DNA and preparing samples for sequencing. Furthermore, this project would not have been possible without the help of various individuals across multiple state, federal, and private agencies who collected tissue samples of northern pike throughout Alaska. I'm thankful to my parents, Wayne and MaryAnn Jalbert who brought me outdoors and sparked my interest in fish and fishing at a young age and have always been there for me. Finally, to my wife, Aili Peyton-Jalbert who tolerated getting married just before my first semester of graduate school then living apart for two years. Your constant encouragement, support, and friendship was key to my success and very much appreciated. This work was supported in part by the high-performance computing and data storage resources operated by the Research Computing Systems Group at the University of Alaska Fairbanks, Geophysical Institute. The project was conducted under UAF Institutional Animal Care and Use Committee protocol # 921163-3 and Alaska Department of Fish and Game fish resource permit # SF2017-168.

General Introduction

Biological invasions of non-native species are a leading cause of extinction (Clavero and Garciaberthou 2005), loss of native biodiversity (Moyle and Leidy 1992; Vitousek et al. 1996; Mooney and Cleland 2001) and erosion of genetic diversity worldwide (Ricciardi and Macisaac 2010). A subset of introduced non-native species become invasive (sensu Davis et al. 2011) and result in environmental damages and economic impacts adding into the billions per year (Pimentel et al. 2005). Although the economic costs of invasions are relatively straightforward to calculate, the ecological impacts are difficult to quantify (Pejchar and Mooney 2009) as they often include indirect effects such as competition with invasive species, predation, and changes in genetic diversity (e.g., hybridization with native species). As such, strategies to guide conservation efforts for native species and management of non-native species must be assessed across broad geographic extents (Vander Zanden et al. 2004; Vander Zanden and Olden 2008; Olden et al. 2011).

Aquatic ecosystems, particularly freshwater, are much more at risk of and sensitive to the impacts of invasion (Moorhouse and Macdonald 2015). Vectors for freshwater species transport include unintentional paths such as ballast water releases (Rahel 2007) and intentional, often illegal, introductions by humans to boost recreational hunting or fishing opportunity (Johnson et al. 2009). Although stocking fish can benefit anglers through increased recreational fishing opportunities in an area, it can lead to detrimental consequences for native fauna including competition with or extirpation of native fishes (Moyle and Light 1996; Johnson et al. 2009). Illegal stocking has led to the rapid range expansion of numerous species and resulted in reduced diversity of freshwater fauna worldwide (Rahel 2002, 2007; Cambray 2003; Fausch and García-Berthou 2013). High propagule pressure, or the number and quantity of individuals introduced

during invasion has been proposed as a mechanism explaining the vulnerability of freshwater systems (Lockwood et al. 2005). Further, human reliance on freshwater systems for agriculture, hydropower, transportation, food, and recreation has led to the modification of river networks worldwide, and increased rates of disturbance, and propagule pressure to facilitate species range expansions (Vitousek et al. 1996; McKinney and Lockwood 1999).

Worldwide invasion and range expansion of the highly predatory northern pike (*Esox lucius; hereafter 'pike'*) have increased since the 1960s (McMahon and Bennett 1996; Johnson et al. 2009), with non-native populations established in 40 states in the United States (Fuller and Neilson 2015). In Alaska, pike are an ecologically and culturally important native fish species north and west of the Alaska Mountain Range, but do not naturally occur south of the range with the exception of what is thought to be a post-glacial relict population near Yakutat, Alaska (Morrow 1980). In the 1950s, a floatplane pilot reportedly introduced pike into the 60 000 km^2 Matanuska-Susitna basin by translocation from the native range (Minto Flats, near Fairbanks, AK) into Bulchitna Lake (Susitna, AK) (Dunker et al. 2018). Additional illegal stocking events occurred in the 1960s into Alexander Lake (Susitna, Alaska, USA) as well as in lakes on Alaska's Kenai Peninsula in the 1970s, resulting in further establishment of pike populations in Southcentral Alaska (Dunker et al. 2018). To date, a broad-scale assessment of introduced pike across Southcentral has not been implemented.

The use of genetics to understand invasions is not new but until recently genetic analyses of non-model organisms most commonly relied on descriptions of patterns of genetic diversity relying on a relatively small number of genetic markers (Rius et al. 2015). However, recent advances in DNA sequencing technology and ancillary molecular biology protocols have greatly reduced the costs of producing DNA sequence data. These novel approaches are increasingly

used in population genomics (see Casillas and Barbadilla 2017), phylogenetics (Emerson et al. 2010, McCormack et al. 2013), wildlife conservation (Angeloni et al. 2012), and environmental monitoring (Shokralla et al. 2012). Although the use of next-generation sequencing (NGS) to address biological invasion issues has been limited, increased access to these technologies has established the utility of NGS for the study of invasions (for discussion: Rius et al. 2015). These tools are poised to revolutionize our understanding of invasions, particularly when the invader has not been extensively studied and is known to impact native fauna.

Introduced populations that result from introductions from multiple sources often express levels of genetic diversity similar to that of native populations (Kolbe et al. 2004). This maintenance of genetic diversity increases the probability that a population will respond positively to environmental change or threats such as reduced resource availability (Jump et al. 2009) since genetically diverse populations are more likely to contain traits that may be advantageous in new environments (Carlson et al. 2014). In contrast, small populations are susceptible to loss of genetic diversity through genetic drift, founder effects, and genetic bottlenecks (Sakai et al. 2001), making them more at risk of failing to establish in novel environments.

Pike throughout its native range exhibit low levels of genetic variability when compared to other fishes throughout their native range (Ward et al. 1994; Wennerström et al. 2018), with slightly higher levels in Eurasian populations, which suggests a Eurasian origin for North American pike populations (Skog et al. 2014). Although pike exhibit low diversity, the species shows high among-population differentiation (Jacobsen et al. 2004) and have been shown to have the highest genetic differentiation as measured by F_{ST} of any freshwater fish (Ward et al. 1994). Low diversity and high differentiation in extant pike populations are likely the result of

their history of post-glacial dispersal and their status as a top predator (Wennerström et al. 2018) which is associated with small population sizes. Thus far, studies of the genetic diversity of invasive pike has been limited in scope (Pedreschi et al. 2014). An examination of the history of invasion into Southcentral Alaska can identify sources of the introduction or corroborate previous knowledge (i.e., that the founder was Minto Flats) and provide a valuable monitoring tool through a genetic baseline. Also, genetic data can provide insight into mechanisms that allow for successful invasion.

While uncovering the history of the invasion is useful, predicting the current and future impacts of invasive pike provides a tool for management of the invasion across large geographic areas. Invasive pike have been linked to the rapid decline of multiple salmonid (salmon and trout) species (Rutz 1999; Dunker et al. 2018) as well as the extirpation of a rare weakly-armored threespine stickleback (*Gasterosteus aculeatus*) population in Prator Lake, Alaska (Patankar et al. 2006; Rutz 1996; 1999; Sepulveda et al. 2015; 2013). Local species extirpations, perhaps due to the naivety of native salmonids to this novel predator (Sih et al. 2010), are likely to continue as pike spread throughout the Matanuska-Susitna basin. Pike and Pacific salmon require slow moving, shallow, well-vegetated aquatic habitats to complete their life cycle and rely on vegetation for larval and juvenile development (Bjornn and Reiser 1991; Casselman and Lewis 1996; Jacobsen and Engström-Öst 2018). The common habitat use (Dunker et al. 2018) and pikes' preference for soft-rayed fishes (Eklöv et al. 1989) leads to heavy predation of juvenile salmonids by pike (Rutz 1999; Sepulveda et al. 2013, 2015). Thus, examining the current distribution of pike, connectivity between sources of pike and the river network, and determining the extent to which salmon and pike may overlap is crucial for predicting the future impacts of the invasion and informing management decisions

Due to the vast scale of management areas and limited resources, estimates of fish habitat potential based on stream geomorphology, termed 'intrinsic potential' (Burnett et al. 2007) have been developed. Intrinsic potential models have been used to predict the distribution of salmonid habitat in the Western United States (Burnett et al. 2007; Bidlack et al. 2014; Matter et al. 2018). Similar to other habitat suitability models (Guisan et al. 2017), intrinsic potential models assign a suitability value for attributes deemed important to a species or life-stage. However, intrinsic potential models rely on relatively static reach-scale attributes (e.g., channel confinement, gradient, or floodplain width) for prediction (Burnett et al. 2007). These reach-scale estimates can be applied at various spatial scales and provide a tool for managers. Although intrinsic potential models allow for identification of quality habitat across broad landscapes, estimates of habitat potential alone cannot describe the vulnerability of Pacific salmon to the invasion of pike in the Matanuska-Susitna basin. Other factors, like the overlap between salmon and pike, connectivity between invaded and un-invaded areas, and vectors for movement are important to consider.

Bayesian networks provide a method for incorporating qualitative and quantitative natural resource data into a formal decision tool and have been used to integrate a variety of data like habitat suitability models (Peterson et al. 2008; Falke et al. 2015) and to provide quantitative solutions to ecological problems (McCann et al. 2006). The integration of various sources of data and tracking of uncertainty through each stage of the network allow for accurate predictions under different scenarios (McCann et al. 2006; Uusitalo 2007). Further utility can be found in their ability to easily incorporate new information, thus reducing uncertainty of the estimates. Taken together, these factors make Bayesian networks a useful tool with which to assess the vulnerability of Pacific salmon to the ongoing invasion by pike, especially since there are

multiple types of information (e.g., habitat data, catch data, professional knowledge) available for the invasion.

It is evident that new methods are needed to predict where invasive species are likely to invade (Dick et al. 2013). However, these new methods must be widely applicable and readily available to managers to be useful. Here, I demonstrate how tools such as intrinsic potential habitat modeling, Bayesian networks, and next-generation sequencing can be employed to investigate invasions and efficiently identify critical areas where management actions will attain the greatest benefits. Further, these tools can be readily adapted for use with other species and areas. Finally, it is likely that pike are not the sole or primary threat to Pacific salmon in Southcentral Alaska, but my results demonstrate a clear connection between pike and salmon in this region. Specifically, as pike continue to invade suitable habitat, they will interact with the Matanuska-Susitna basins' naïve salmon and will further impact already struggling salmon returns.

The pairing of intrinsic potential models and connectivity with the reconstruction of the genetic history of this invasion will provide estimates of current pike distribution, identify suitable sites of invasion, provide insight into colonization history, and establish a genetic baseline of non-native pike in Southcentral Alaska. Together, these data offer insight into the overall invasive potential of the species and provide managers with the tools necessary to identify unaffected, vulnerable habitat throughout Southcentral Alaska and monitor for new introduction events.

References

Bidlack, A. L., L. E. Benda, T. Miewald, G. H. Reeves, and G. McMahan. 2014. Identifying suitable habitat for chinook salmon across a large, glaciated watershed. Transactions of the American Fisheries Society 143(3):689–699.

Bjornn, T., and D. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83–138 *in* W. R. Meehan, editor. Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats. American Fisheries Society Special Publication.

Burnett, K. M., G. H. Reeves, D. J. Miller, S. Clarke, K. Vance-Borland, and K. Christiansen. 2007. Distribution of salmon-habitat potential relative to landscape characteristics and implications for conservation. Ecol Appl 17(1):66–80.

Cambray, J. A. 2003. Impact on indigenous species biodiversity caused by the globalisation of alien recreational freshwater fisheries. Hydrobiologia 500:217–230.

Carlson, S. M., C. J. Cunningham, and P. A. H. Westley. 2014. Evolutionary rescue in a changing world. Trends in Ecology and Evolution 29(9):521–530. Elsevier Ltd.

Casselman, J. M., and C. A. Lewis. 1996. Habitat requirements of northern pike (E*sox lucius*). Canadian Journal of Fisheries and Aquatic Sciences 53(S1):161–174.

Clavero, M., and E. Garciaberthou. 2005. Invasive species are a leading cause of animal extinctions. Trends in Ecology & Evolution 20(3):110–110.

Davis, M. A., M. K. Chew, R. J. Hobbs, A. E. Lugo, J. J. Ewel, G. J. Vermeij, J. H. Brown, M. L. Rosenzweig, M. R. Gardener, S. P. Carroll, K. Thompson, S. T. A. Pickett, J. C. Stromberg, P. Del Tredici, K. N. Suding, J. G. Ehrenfeld, J. Philip Grime, J. Mascaro, and J. C. Briggs. 2011. Don't judge species on their origins. Nature 474(7350):153–154.

Dick, J. T. A., M. E. Alexander, J. M. Jeschke, A. Ricciardi, H. J. MacIsaac, T. B. Robinson, S. Kumschick, O. L. F. Weyl, A. M. Dunn, M. J. Hatcher, R. A. Paterson, K. D. Farnsworth, and D. M. Richardson. 2013. Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. Biological Invasions 16(4):735–753.

Dunker, K. J., A. J. Sepulveda, R. L. Massengill, and D. S. Rutz. 2018. The northern pike, a prized native but disastrous invasive. Pages 356–398 *in* C. Skov and P. A. Nilsson, editors. Biology and Ecology of Pike, 1st edition. CRC Press, Boca Raton.

Eklöv, P., S. F. Hamrin, and P. Eklov. 1989. Predatory efficiency and prey selection: interactions between pike E*sox lucius*, perch P*erca fluviatilis* and rudd *Scardinus erythrophthalmus*. Oikos 56(2):149.

Falke, J. A., R. L. Flitcroft, J. B. Dunham, K. M. McNyset, P. F. Hessburg, and G. H. Reeves. 2015. Climate change and vulnerability of bull trout (*Salvelinus confluentus*) in a fire-prone landscape. Canadian Journal of Fisheries and Aquatic Sciences 72(2):304–318.

Fausch, K. D., and E. García-Berthou. 2013. River conservation: challenges and opportunities. Pages 193–215 *in* S. Sabater and A. Elosegi, editors. The problem of invasive species in river ecosystems, 1st edition. Fundación BBVA.

Fuller, P. L., and M. Neilson. 2015. *Esox lucius* Linnaeus, 1758: u.s. geological survey, nonindigenous aquatic species database. U.S. Geological Survey, Gainesville, FL. https://nas.er.usgs.gov/queries/FactSheet.aspx?speciesID=676.

Guisan, A., W. Thuiller, and N. Zimmermann. 2017. Overview, principles, theory, and assumptions behind habitat suitability modeling. Pages 9–58 In Habitat Suitability and Distribution Models: With Applications in R. Cambridge University Press., Cambridge.

Jacobsen, B. H., M. M. Hansen, and V. Loeschcke. 2004. Microsatellite dna analysis of northern pike (*Esox lucius* L.) populations: insights into the genetic structure and demographic history of a genetically depauperate species. Biological Journal of the Linnean Society 84(1):91–101.

Jacobsen, L., and J. Engström-Öst. 2018. Coping with environments; vegetation, turbidity and abiotics. Pages 32–61 *in* C. Skov and P. A. Nilsson, editors. Biology and Ecology of Pike, 1st edition. CRC, Boca Raton.

Johnson, B. M., R. Arlinghaus, and P. J. Martinez. 2009. Are we doing all we can to stem the tide of illegal fish stocking? Fisheries 38(8):389–394.

Jump, A. S., R. Marchant, and J. Peñuelas. 2009. Environmental change and the option value of genetic diversity. Trends in Plant Science 14(1):51–58.

Kolbe, J. J., R. E. Glor, L. Rodríguez Schettino, A. C. Lara, A. Larson, and J. B. Losos. 2004. Genetic variation increases during biological invasion by a cuban lizard. Nature 431(7005):177–181.

Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20(5):223–228.

Matter, A. N., J. A. Falke, J. A. López, and J. W. Savereide. 2018. A rapid-assessment method to estimate the distribution of juvenile Chinook salmon in tributary habitats using edna and occupancy estimation. North American Journal of Fisheries Management 38(1):223–236.

McCann, R. K., B. G. Marcot, and R. Ellis. 2006. Bayesian belief networks: applications in ecology and natural resource management. Canadian Journal of Forest Research 36(12):3053–3062.

McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution 14(11):450–453.

McMahon, T. E., and D. H. Bennett. 1996. Walleye and northern pike: boost or bane to northwest fisheries? Fisheries 21(8):6–13.

Mooney, H. A., and E. E. Cleland. 2001. The evolutionary impact of invasive species. Proceedings of the National Academy of Sciences 98(10):5446–5451.

Moorhouse, T. P., and D. W. Macdonald. 2015. Are invasives worse in freshwater than terrestrial ecosystems? Wiley Interdisciplinary Reviews: Water 2(1):1–8.

Morrow, J. E. 1980. The freshwater fishes of Alaska. Alaska Northwest Publishing Company, Anchorage.

Moyle, P. B., and R. A. Leidy. 1992. Loss of biodiversity in aquatic ecosystems: evidence from fish faunas. Pages 127–169 *in* P. L. Fiedler and S. K. Jain, editors. Conservation Biology The Theory and Practice of Nature Conservation and Management, 1st edition. Chapman and Hall, New York and London.

Moyle, P. B., and T. Light. 1996. Biological invasions of fresh water: empirical rules and assembly theory. Biological Conservation 78(1–2):149–161.

Olden, J. D., M. J. Vander Zanden, and P. T. J. Johnson. 2011. Assessing ecosystem vulnerability to invasive rusty crayfish (*Orconectes rusticus*). Ecological Applications 21(7):2587–2599.

Pedreschi, D., M. Kelly-Quinn, J. Caffrey, M. O'Grady, S. Mariani, and A. Phillimore. 2014. Genetic structure of pike (*Esox lucius*) reveals a complex and previously unrecognized colonization history of ireland. J Biogeogr 41(3):548–560.

Pejchar, L., and H. A. Mooney. 2009. Invasive species, ecosystem services and human well-being. Trends in Ecology and Evolution 24(9):497–504.

Peterson, D. P., B. E. Rieman, J. B. Dunham, K. D. Fausch, and M. K. Young. 2008. Analysis of trade-offs between threats of invasion by nonnative brook trout (S*alvelinus fontinalis*) and intentional isolation for native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). Canadian Journal of Fisheries and Aquatic Sciences 65(4):557–573.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the united states. Ecological Economics 52(3):273–288.

Rahel, F. J. 2002. Homogenization of freshwater faunas. Annual Review of Ecology and Systematics 33(1):291–315.

Rahel, F. J. 2007. Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. Freshwater Biology 52(4):696–710.

Ricciardi, A., and H. J. Macisaac. 2010. Impacts of biological invasions on freshwater ecosystems. Pages 211–224 *in* D. M. Richardson, editor. Fifty Years of Invasion Ecology.

Rutz, D. S. 1999. Movements, food availability and stomach contents of northern pike in selected Susitna River drainages, 1996-1997. Anchorage.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. Mccauley, P. O. Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive specie source: annual review of ecology and systematics. Annual Reviews Stable 32:305–332.

Sepulveda, A. J., D. S. Rutz, A. W. Dupuis, P. A. Shields, and K. J. Dunker. 2015. Introduced northern pike consumption of salmonids in southcentral Alaska. Ecology of Freshwater Fish 24(4):519–531.

Sepulveda, A. J., D. S. Rutz, S. S. Ivey, K. J. Dunker, and J. A. Gross. 2013. Introduced northern pike predation on salmonids in southcentral Alaska. Ecology of Freshwater Fish 22(2):268–279.

Sih, A., D. I. Bolnick, B. Luttbeg, J. L. Orrock, S. D. Peacor, L. M. Pintor, E. Preisser, J. S. Rehage, and J. R. Vonesh. 2010. Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos 119(4):610–621.

Skog, A., L. A. Vøllestad, N. C. Stenseth, A. Kasumyan, and K. S. Jakobsen. 2014. Circumpolar phylogeography of the northern pike (E*sox lucius*) and its relationship to the amur pike (*e. reichertii*). Frontiers in Zoology 11(1):67.

Uusitalo, L. 2007. Advantages and challenges of bayesian networks in environmental modelling. Ecological Modelling 203(3–4):312–318.

Vitousek, P. M., C. M. DAntonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist 84(5):468–478.

Ward, R. D., M. Woodwark, and D. O. F. Skibinski. 1994. A comparison of genetic diversity levels in marine, freshwater, and anadromous fishes. Journal of Fish Biology 44(2):213–232.

Wennerström, L., D. Bekkevold, and L. Laikre. 2018. Population genetics of pike. Pages 164–184 *in* C. Skov and P. A. Nilsson, editors. Biology and Ecology of Pike, 1st edition. CRC Press, Boca Raton.

Vander Zanden, M. J., and J. D. Olden. 2008. A management framework for preventing the secondary spread of aquatic invasive species. Canadian Journal of Fisheries and Aquatic Sciences 65(7):1512–1522.

Vander Zanden, M. J., J. D. Olden, J. H. Thorne, and N. E. Mandrak. 2004. Predicting occurrences and impacts of smallmouth bass introductions in north-temperate lakes. Ecological Applications 14(1):132–148.

THIS PAGE INTENTIONALLY LEFT BLANK

Chapter 1: Evidence of genetic structure despite low genetic diversity in an invasive apex predator, the northern pike (*Esox lucius*)[1]

Abstract

In this paper, we examine the genetic structure of invasive populations of northern pike (*Esox lucius*) in Southcentral Alaska and provide insight into its invasion history using a genotyping by sequencing strategy. We determined genotypes at 7,889 single nucleotide polymorphisms (SNPs) from three native and seven invasive populations from the Susitna River basin and Kenai Peninsula in Southcentral Alaska. We detected low levels of genetic variability in native populations (mean heterozygosity = 0.0360 and mean π = 0.000241) and even lower diversity in introduced populations (mean heterozygosity = 0.0227 and mean π = 0.000131), which suggests small founding population sizes during introduction. We identified high differentiation among some populations with global F_{ST} = 0.424 and little admixture between populations, which we attribute to founder effects, genetic drift of numerically small populations, and negligible effective migration rates. Clustering analyses (i.e., Bayesian clustering, PCA) identified five populations among the sampled locations. The five groups consisted of three distinct native populations, one group comprised samples from five invasive sites in the Susitna drainage, and one group comprised two sites on the Kenai Peninsula. The genotype dataset did not provide a clear links between specific native and invasive groups, although it did provide evidence for different founding sources for the Kenai and Susitna groups.

[1] Jalbert, C.S., López, J.A., Falke, J.A., Westley, P.A.H, and Dunker, K.J. 2018. Evidence of genetic structure despite low genetic diversity in an invasive apex predator, the northern pike (*Esox lucius*). Formatted for the journal *Evolutionary Applications*.

Introduction

Biological invasions of non-native species are a leading cause of extinction (Clavero and Garciaberthou 2005), loss of native biodiversity (Moyle and Leidy 1992; Vitousek et al. 1996; Mooney and Cleland 2001) and loss of genetic diversity worldwide (Ricciardi and Macisaac 2010). The subset of introduced non-native species that produce environmental impacts and thus become invasive (sensu Davis et al. 2011) translate to substantial economic impacts, with the latter tallying into the billions of US dollars per year (Leung et al. 2002; Pimentel et al. 2005). Invasive species can outcompete native species for prey, directly prey upon native taxa, and hybridize with native populations resulting in native genetic diversity loss (Vander Zanden et al. 2004; Muhlfeld et al. 2009; Ricciardi and Macisaac 2010). However, invasions also provide opportunities to assess underlying ecological and evolutionary processes in natural settings (Westley 2011). Processes such as mutation, natural selection, gene flow, and genetic drift combine to shape genetic diversity and influence evolutionary potential and survival of organisms. As a result, examination of these processes across broad landscapes can provide insight into factors that facilitate invasions.

One crucial aspect of invasions, propagule pressure, describes the number and quality of individuals introduced in the early stages of invasion and is fundamental to understand invasion success and levels of admixture (Lockwood et al. 2005). Introduced populations that result from high propagule pressure often maintain levels of genetic diversity similar to those of native populations (Kolbe et al. 2004). This maintenance of genetic diversity increases the probability that a population will persist through contemporary adaptive evolution following an environmental change that results in maladaptation (Carlson et al. 2014). In contrast, species

introductions are often a result of small population sizes and are susceptible to loss of genetic diversity through genetic drift, founder effects, and genetic bottlenecks (Sakai et al. 2001).

Worldwide introductions of the highly predatory northern pike (*Esox lucius*; hereafter *'pike'*) outside their native range have increased over the past few decades (McMahon and Bennett 1996; Johnson et al. 2009). As a prized sportfish and common target of aquaculture enhancement and stocking, the invasion of pike into new areas is the product of a combination of natural and human-assisted vectors. Pike are generalist feeders that can tolerate a range of environmental conditions; thus, the species inhabits a wide array of habitats from freshwater to brackish water (Inskip 1982; Raat 1988; Skov et al. 2018). Phenotypic flexibility in pike appears to exist despite low levels of genetic variability, and indeed pike are genetically depauperate when compared to other freshwater fishes (Wennerström et al. 2018). For instance, Seeb et al. (1987) found that only two of 65 allozyme loci were polymorphic in eight North American populations ranging from western Canada to the Mississippi River Drainage. Similarly, mitochondrial and microsatellite markers revealed little variation throughout the Holarctic, although slightly higher levels of genetic diversity in Eurasian populations was suggestive of a Eurasian origin for North American pike populations (Skog et al. 2014). European populations show low genetic variability but exhibit high differentiation between populations. This low diversity has been attributed to low population sizes that resulted from post-glacial bottlenecks which shaped present day population structure (Jacobsen et al. 2004). A historical analysis of genetic variation revealed low effective population sizes, with losses in heterozygosity of around 8% over a 32-year study period (Miller and Kapuscinski 1997). The extremely low levels of genetic variability found in pike are likely a result of their post-glacial dispersal patterns, in which pike radiated outward from a few refugia, and their status as a top predator. In summary,

pike exhibit low levels of genetic diversity throughout their natural range, when compared to other freshwater fishes (Appendix B).

In Alaska, pike are an ecologically and culturally important native fish species north and west of the Alaska Mountain Range, but do not naturally occur south of the range except for what is thought to be a single isolated post-glacial relict population near Yakutat, Alaska (Morrow 1980). In the 1950s, a floatplane pilot reportedly removed pike from the native range (Minto Flats, near Fairbanks, AK, USA) and released the fish into Bulchitna Lake (Susitna, AK, USA) with the intention to hold recreational fishing contests (Bulchitna Lake residents, *personal communication*, 2017). A small dam at the outlet of Bulchitna Lake was constructed to contain pike in the lake, but presumably high-water events flooded the lake allowing access to the Susitna River drainage (Figure 1). This illegal stocking event is thought to be the initial source of pike in the Matanuska-Susitna basin (Haught and von Hippel 2011; Dunker et al. 2018). Additional illegal stocking events occurred in the 1960s into Alexander Lake (Susitna, Alaska, USA) as well as in lakes on the Kenai Peninsula (1970s), promoting the establishment of non-native pike populations (Dunker et al. 2018). Despite widespread concern about the impacts of pike, particularly on native Pacific salmonids (*Oncorhynchus* spp.), and their position as the putative link between European and North American lineages, virtually nothing is known about the genetic diversity of pike in Alaska. A few studies have included samples from Alaskan pike but were unable to or did not differentiate between populations within Alaska (Seeb et al. 1987; Skog et al. 2014; Wooller et al. 2015). Here, we expand knowledge about pike populations within Alaska with an emphasis on invasive pike, using the largest marker set for pike to date.

Our overall goal was to examine the history of the invasion into Southcentral Alaska to identify potential sources of the introduction and to provide baseline genetic data for invasive

pike. To do this we examined genetic variability, population affinities, and genetic diversity of native and invasive pike throughout Alaska. Our objectives were to 1) characterize genetic variability of native and introduced populations, and 2) determine the affinities between native and introduced populations. We expected that introduced populations resulting from a single introduction event would exhibit less genetic diversity than native populations.

Materials and methods

Sampling

We collected northern pike from ten sites comprising three locations from within the species' native range and seven from the non-native range (Table 1). We selected invasive sites based on: 1) previous knowledge of human-mediated introduction, 2) the spatial relationship to known introduction sites, and 3) the relative importance to Pacific salmon in the area. We selected native sites based on the likelihood of representing a source population for the invasion into Southcentral Alaska (Dunker et al. 2018).

Pike were captured using a combination of gillnet, seine net, rotenone treatment, and angling. All pike captured in the invasive range and 50 pike from each native site were euthanized. Pectoral fin clip tissues were placed in reagent alcohol (95%) or a solution of dimethyl sulfoxide (DMSO), Ethylenediaminetetraacetic acid (EDTA), and salt for preservation (Seutin et al. 1991) immediately after collection. Sample collection and associated protocols were approved by the Alaska Department of Fish and Game (ADF&G) and the Institutional Animal Care and Use Committee (IACUC) and were collected under Fish Resource Permit number SF2017-168 and IACUC protocol number 921163-3.

Genomic DNA isolation

Total genomic DNA was isolated from preserved tissue samples using the reagents and protocols of the Qiagen Gentra Puregene Tissue kit (QIAGEN Inc., Valencia CA) with a modification to the final elution buffer. Specifically, isolated genomic DNA was dissolved in 50 µL of low-EDTA TE buffer (pH 8.0) to minimize potential inhibition of downstream reactions. Quantity and purity of DNA preparations were assessed through fluorometry, spectrophotometry and electrophoresis.

DNA sequencing

We used a double digest restriction-site associated sequencing (ddRAD-seq) approach (Peterson et al. 2012) to broadly characterize genetic variation from 200 pike individuals from seven non-native sites (n = 105) and three native sites (n = 95; Table 1). A sample size of 10 – 25 randomly selected individuals per site was based on previous studies that used ddRAD-seq datasets to determine genetic diversity (Hale et al. 2012; Willing et al. 2012). Briefly, ≥ 200 ng of DNA from each sample, was digested using the restriction enzyme combination MspI (C|CGG) and EcoRI (G|AATTC). Restriction digest products were used to build individually tagged libraries, which were then pooled, and size selected base pair inserts and sequenced on an Illumina HiSeq platform using 2x125bp PE V4 chemistry. Library construction, sequencing, and demultiplexing was performed by GENEWIZ LLC (South Plainfield, NJ, USA).

Sequence data quality assessment

We used FASTQC version 0.11.7 (Andrews 2010) to assess the quality of the sequence reads and MULTIQC version 1.5 (Ewels et al. 2016) to obtain a consolidated summary of individual FASTQC module reports. Sequences and individuals with more than 20% of the bases exhibiting a Phred quality score (i.e., base calling accuracy) less than Q30 were removed from

downstream analyses. These data demonstrated that our choice of restriction enzymes was appropriate and did not introduce significant biases as the average GC (guanine-cytosine) content of our reads (44.5%) was similar to the reference genome (42.2%).

Genotyping

The *ipyrad* (v 0.7.23, available: https://ipyrad.readthedocs.io/index.html) pipeline was used to identify sequenced loci from the ddRAD-seq sequencing output and to create aligned datasets of genotypes. The analysis pipeline includes tools to assist with quality trimming and adapter removal, *de novo* and reference-based assembly of RAD loci, read mapping, SNP calling, and baseline data filtering. To produce a set of aligned genotyped loci, we aligned ddRAD-seq reads to the pike genome assembly (Eluc_V3, Rondeau et al. 2014) using the *ipyrad* pipeline. We assembled sequences using default parameters with the following modifications: "pairddrad" reference-based assembly settings: restriction enzyme overhang to filter adapter (AATTC, CGG); level of similarity at which two sequences are homologous (0.85); removal of Illumina adapters (0); trim N bases from beginning and end of R1 and R2 reads (0, 0, 0, 0); and trim N bases from 5' or 3' end of final loci (0, 0, 0, 0). To restrict the output to loci that are shared across 70% of samples (N = 140) we invoked the "min_samples_locus" parameter.

The pipeline created a final dataset in filetypes readable by standard population genetics software (e.g., VCF). Statistical analyses were completed using packages within R version 3.5.1 (R Core Team 2018) and VCFTOOLS version 0.1.15 (Danecek et al. 2011). All custom pipelines and R scripts are available upon request.

Genetic variability

To estimate genetic variability, we examined the number of private alleles found in each location, proportion of polymorphic loci in each location, π (nucleotide diversity), and observed

(H_O) and expected (H_E) heterozygosity. A count of private alleles, the proportion of polymorphic loci found in each location, nucleotide diversity (Nei and Li 1979), and heterozygosity (H_O) was calculated using the R package *radiator* version 0.0.16 (Gosselin 2017) and verified using other, common genetic software (e.g., *hierfstat*, POPULATIONS).

Population structure and genetic differentiation

To examine the genetic differentiation between populations and identify potential founding populations, we calculated the average pairwise F_{ST} values between all ten locations (Table 3). Estimates of genetic differentiation between each sampling location were calculated using Weir and Cockerham's F_{ST} estimator (Weir and Cockerham 1984) within the R package *hierfstat* version 0.04-22 (Goudet 2005), using the pairwise.WCfst function. One thousand bootstraps were carried out to determine the 95% confidence intervals for each pair of populations and across all loci to evaluate statistical significance of estimated values. Bootstrapping was performed with the boot.ppfst function in *hierfstat*.

The Bayesian clustering analysis within STRUCTURE version 2.3.4 (Pritchard et al. 2000) was used to infer the presence of populations and assign individuals to populations. An initial analysis of genetic structure was performed among all individuals without prior location information. Additional analyses were performed using location information in a hierarchical fashion to assess fine-scale population structure. We used a burn-in of 100,000 and 10,000 Markov Chain Monte Carlo repetitions after the burn-in, then tested values of K from 1 to 15 with 20 independent replicates of each K-value. We used the StrAuto pipeline version 1.0 (Chhatre and Emerson 2017) to parallelize STRUCUTRE analyses and used the Evanno ΔK method (Evanno et al. 2005), then visualized results with STRUCTURE HARVESTER version 0.6.94 (Earl and vonHoldt 2012). Finally, to generate a consensus for our replicate K-runs, we

used CLUMPAK version 1.1 (Kopelman et al. 2015), which relies on DISTRUCT (Rosenberg 2004) for visualization. The program uses a Markov clustering algorithm to assist in the comparison of model results across different K-values with optimal values of K identified by comparing the ΔK method and the highest log-likelihood ln(Pr(X|K)) result. We also used a discriminant analysis of principal components (DAPC) as implemented in the R package *adegenet* (Jombart 2008) to estimate variability and optimal number of clusters without genetic model-based assumptions (e.g., Hardy-Weinberg equilibrium). We used the find.clusers() function, found in *adegenet,* to determine the number of population clusters (K). In short, the model identifies the optimum K by maximizing the variation between groups and iterates over a sequential number of values for K while comparing solutions using the Bayesian Information Criterion (BIC). To avoid overfitting the DAPC, we selected the optimal number of principal components (PCs) using the cross-validation function in *adegenet.* We replicated the cross-validation 100 times and used a training data set of 80% to predict the group membership of individuals under a variable number of PCs. The optimal number of PCs was selected based on the lowest root mean squared error. Finally, to verify our previous analysis, we selected the best K by examining the rate of change in BIC, where the optimal BIC was chosen as the lowest value. Our independent BIC analysis produced similar estimates of K to those obtained using DAPC so only the results from the DAPC are reported here.

Phylogenetic relationships

The phylogenetic relationship between locations was assessed by reconstructing a distance tree based on the neighbor-joining algorithm (Saitou and Nei 1987). We assessed the support for each branch length using 100 bootstraps. Due to the absence of a known outgroup population in our dataset, we used midpoint method to root the tree (Farris 1972) as an approximation to the true

placement of root. Here, the neighbor-joining algorithm was calculated using Nei's distance (Nei 1978) as implemented within *poppr* using a custom R-script. Trees were visualized using the R package *ggtree* (Yu et al. 2017) and FigTree (available: http://tree.bio.ed.ac.uk/software/figtree/).

Results

Data summary

We generated ddRAD-seq data from 200 individuals from ten sites across Alaska including sites within the species native (3 sites, n = 70) and introduced range (7 sites, n = 130). The average number of fish sequenced at each location was 20 (range 10 – 25). The average sequencing yield per individual was 5 million reads (range 3.6 to 6.6) representing an average of 1.25 Gbases per individual (± 0.12 Gbases [SD]) . All sequences had mean Phred Q-scores above 30 (mean = 38 ± 0.7 [SD]) and 91.62% of all base calls had a quality score above 30. The average GC content of all reads was 44.5% (± 2.6% [SD]).

The *ipyrad* pipeline identified a total of 52,441 loci and retained 16,145 post filtering, with an average of 14,915 (± 380 [SD]) loci per individual. The following sequence of filters were applied by the genotype assembly pipeline with the number of reads lost to each listed in parenthesis (Table S1): duplicates removed (849); loci exceeding threshold of insertions/deletions removed (815); loci exceeding threshold of variable sites removed (589); loci exceeding threshold of observed heterozygosity removed (300); loci failing to reach minimum number of individuals genotyped removed (34,773); loci exceeding threshold of observed alleles removed (1,332). After further filtering for biallelic and variant-only sites, we produced a VCF comprising 7,889 high-quality SNPs from our sample set.

Genetic variability

The number of private alleles in each population was assessed to provide insight into population relationships (i.e., gene flow and ancestry). Native pike populations held an average of 891 (± 13 [SD]) private alleles which is significantly more than ($t(198) = -76.7$, $p = 0.0001$) what was found in invasive pike populations (mean = 324 ± 61 [SD]; Table 2). Estimates of nucleotide diversity for all locations ranged from 8.45×10^{-5} (Otter Lake; OTT) to 2.51×10^{-4} (Lake Nerka; NKA), with an average of 2.73×10^{-4}. Nucleotide diversity was higher in native populations (mean = $2.41 \times 10^{-4} \pm 1.03 \times 10^{-5}$ [SD]) than in invasive populations (mean = $1.31 \times 10^{-4} \pm 4.39 \times 10^{-4}$ [SD]). Similarly, the percentage of polymorphic loci was higher in native populations (mean = 33.7% ± 2.3% [SD]) than in invasive populations (mean = 13.4% ± 1.3% [SD]). The least polymorphic location was Otter Lake (12%) and the most polymorphic location was Lake Nerka (36%).

For all populations and loci, the average observed heterozygosity was lower than expected. Heterozygosity ranged from 0.0153 (Otter Lake) to 0.0547 (Lake Nerka), with a mean of 0.0326 (± 0.0268 [SD]). Mean levels of heterozygosity for the two Kenai Peninsula populations (0.0278) fell between the Susitna and native populations. However, overall, introduced populations had lower heterozygosity (mean = 0.0227 ± 0.0041 [SD]) than native populations (mean = 0.036 ± 0.0047 [SD]); $t(198) = -20.774$ $p = 0.0001$.

Population structure and genetic differentiation

The pairwise F_{ST} varied widely between comparisons ranging from 0.668 to 0.047 with a global F_{ST} of 0.424. The highest pairwise F_{ST} values were between Tiny Lake (Kenai Peninsula, Alaska) and Otter Lake (Anchorage, Alaska) with $F_{ST} = 0.668$ and the lowest between Alexander Lake and Alexander Creek (Susitna basin, Alaska) with $F_{ST} = 0.047$. We grouped the six invasive

locations from the Susitna basin and Anchorage into a "Susitna" group and both invasive locations from the Kenai Peninsula into a "Kenai" group for comparison with the three native populations ("Native"). The F_{ST} between the Susitna and Native groups was 0.0812 while F_{ST} between Kenai and Native groups was 0.0596. Curiously, F_{ST} between the two invasive groups (i.e., Susitna and Kenai) was much higher at 0.1889, suggesting highly differentiated populations and different origins. This result was supported by location-based pairwise comparisons which were much higher between Kenai-Susitna invasive pairs, than invasive-native pairs (Table 3).

The STRUCTURE analysis identified K = 2 as the highest log-likelihood for our full dataset (Figure 3). The two groups were 1) the Susitna basin invasive locations and 2) the native and Kenai Peninsula (invasive) locations. We split our samples into the two groups identified by analysis of the full sample set (Figure 3) to look at fine scale structure. For the group composed of fish from all Susitna basin sites, there was a lack of consensus between estimates of K using methods outlined by Evanno and the log-likelihood method. The two methods produced wildly different results from K = 2 to K = 10. Hence, we failed to identify population structure among the invasive pike populations of the Susitna basin. For the second group, there was a consensus of K = 4 through both methods. Initially, the Kenai Peninsula invasive locations diverged from the native populations at K = 2, then the Fairbanks populations split from the remaining western Alaska native populations, and finally the two Western Alaska populations are differentiated (Figure 3). Finally, there was little evidence of admixture throughout all STRUCTURE analyses, suggesting a lack of gene flow between identified groups.

After cross-validation, 20 principal components and four discriminant functions were retained for the DAPC which identified K = 5 as the number of groups for the dataset. All locations had 100% membership probability in the five clusters. The five groups consisted of

three distinct clusters representing each the three sampled native populations, one cluster representing all sampled introduced Susitna basin populations, and a cluster representing the two sampled introduced Kenai Peninsula populations (Figure 2). The distinction between invasive groups on the Kenai Peninsula and Susitna basin was supported by high pairwise F_{ST} values between the two locations.

Phylogenetic relationships

The midpoint rooted tree (Figure 4) aligned with our estimates of K from the DAPC approach. There were five major groups identified by the tree, with three distinct clusters for the native locations and one each for the Susitna and Kenai invasive groups. The native and Kenai Peninsula invasive locations showed no evidence of mixture between the groups. In contrast, the Susitna basin group showed no clear phylogenetic structure, with fish from the six sites forming a singled mixed clade.

Discussion

We employed a genotyping by sequencing strategy using the ddRAD-seq technique to examine the genetic variability in native and introduced populations of the northern pike. We genotyped 200 individuals from ten populations in Alaska. We used this dataset to examine the history of the invasion into Southcentral Alaska and attempted to determine population affinities for seven invasive populations. This study provided the first baseline information useful to understand the genetic consequences of bottlenecks on introduced pike in Alaska. Species invasions are generally characterized by dramatic reductions in genetic diversity due to the genetic bottleneck associated with small founding populations, thus the study of genetically depauperate species may help to elucidate factors facilitating invasion success.

We found that native populations had a much higher number of private alleles than invasive populations suggesting a bottleneck due to the introduction event (Kinziger et al. 2011). Generally, the number of private alleles found in invasive populations was consistent and similar among closely located sites suggestive of introduction sources and contemporary gene flow. Interestingly, we found pike in Alexander Creek exhibited more private alleles than pike in its headwater lake, Alexander Lake (Susitna, Alaska, USA), and measures of differentiation between the groups were significantly different than zero ($F_{ST} = 0.047 \pm 0.011$).We interpret this to mean that in the Alexander system, pike from the lake may not frequently migrate into the creek and vice-versa. Our results are generally consistent with telemetry studies by the Alaska Department of Fish and Game where only 7% of all radio-tagged adult pike left the lake and traveled downstream into the creek (Alaska Department of Fish and Game, *unpublished data*). This result generally supports the management actions to suppress pike in the creek as movement from the lake appears to be restricted.

To identify genetic structure and examine among-population variation, we used Bayesian model-based approaches in STRUCTURE and measures of F_{ST}. Divergence between invasive populations in the Susitna basin and native populations was identified at K = 2, signifying differentiation between the two major groups. However, counter to expectation at the K=2 level of clustering the Kenai Peninsula introduced populations remained grouped with the native populations, which indicates different source populations for the Susitna invasive group. A subsequent fine-scale analysis identified differentiation between the Kenai Peninsula introduced populations and the native populations at K = 2 thus, this analysis does not provide evidence for a particular source for the introduction to the Kenai Peninsula. Further, our analyses identified almost no mixture between these groups (Figure 3). A separate analysis of populations

introduced to the Susitna basin failed to identify clear population structure. The lack of structure makes sense under the assumption that there were a limited number of introduction events consisting of a small number of individuals. Under this scenario, pike introduced in the 1950s would have spread from a single location and undergone genetic drift, which without gene flow from native populations would have led to divergence of the groups. Further, the lack of structure provides some indication that the sampled populations were part of the original introduction in the 1950s and not supplemented by subsequent introductions. Future analyses including more populations and potentially more factors impacting genetic structure may help to elucidate the number of introductions. For example, a comprehensive study of the landscape genetics of pike in the St. Lawrence River system revealed low genetic structure between populations with the upper sections of the system showing significantly higher differentiation than populations in the lower section (Ouellet-Cauchon et al. 2014). Their analysis provided insight into the impacts of environmental factors in determining genetic structure within populations of pike which is something we were unable to consider.

We identified a range of pairwise F_{ST} values between locations with some reaching $F_{ST} \sim 0.668$. Pairwise F_{ST} among collections from the Susitna basin were lower (average 0.12) than among the invasive sites from the Kenai Peninsula (0.16) but were similar to the native sites ($F_{ST} = 0.33$). The highest F_{ST} values observed were between the invasive populations from the Kenai Peninsula and Susitna basin, adding support to a scenario of distinct sources for these two introductions. The highly divergent values are supported by our other analyses (e.g., STRUCTURE and DAPC) and led us to the hypothesis that the invasive populations are a result of independent introductions. This idea is supported by a two-decade gap in the first detection of these groups, with pike in the Susitna basin first detected in the 1950s and pike on the Kenai

Peninsula detected in the 1970s. Distance between populations is known to be potentially confounding in characterizing population structure due to the detection of differentiation mediated by the effects of distance on effective migration rather than by reproductive barriers. gene flow. Our data provides an example of the opposite, where geographically distant populations are more closely related than populations that are located closer together. An explanation for this could be that the introduced populations were from different origins which contain some differentiation and were small so random losses in variation due to drift resulted in further differentiation.

We were unable to positively determine population affinities for invasive pike within Southcentral Alaska. Our phylogenetic analyses allowed for a visualization of groups of populations, which matched the DAPC clusters. However, our analyses provided some evidence that the Kenai Peninsula and Lake Clark pike were linked, perhaps with Lake Clark acting as a founder population. Similar to our other analyses, phylogenetic analyses failed to detect population structure between populations in the Susitna basin, signifying a lack of diversity. Further phylogenetic examination of our data as sequences instead of SNPs, using a likelihood rather than genetic distance approach, may help to inform the relationships between the Kenai Peninsula and Native pike populations.

In a review of freshwater fish diversity, pike were found to show low levels of genetic diversity, but the highest divergence of all fish species examined with eight populations from five drainages throughout North America with an F_{ST} equal to 0.852 (data from Seeb et al. 1997; for discussion see Ward et al. 1994). Our analyses also identified populations with high F_{ST} values, suggesting that this pattern may be diagnostic for pike. With regard to genetic diversity, our results were consistent with previous studies that identified pike as a genetically poor species

(Ward et al. 1994; Wennerström et al. 2018). However, we demonstrated additional reductions in genetic diversity within introduced populations in two geographically distinct areas of Southcentral Alaska, the Kenai Peninsula and Susitna River basin. These data were consistent with a founder event in which a small number of pike were released and subsequently spread throughout the system. Similar to other freshwater fishes now found in northern North America, pike survived the Pleistocene glaciation in refugia, expanding as ice retreated, which led to the reduced diversity and higher divergence when compared to marine or anadromous fishes (Ward et al. 1994). Multiple theories to explain reduction in diversity of freshwater fishes have been proposed and could apply to pike. The first is that due to greater physical barriers to movement within river networks than in the ocean, limited dispersal throughout the network resulted in low gene flow, thus isolating populations. Also, populations of top predators are expected to have low population sizes and be subject to strong cycles of abundance due to shifts in food resources (Craig 1996).

Currently, our study is limited in the extent to which we can draw conclusions about structure within the native range based on only three native populations. We acknowledge this shortcoming, but are confident that the populations we included are important as they have been identified as potential founder populations for the introduction into Southcentral Alaska (Dunker et al. 2018) and are known float plane destinations from the Susitna basin and the Kenai Peninsula (Schwoerer 2017). Also, to extend our work and assess broader questions of Alaskan glacial refugia (see Miller and Senanan 2003), population structure of North American pike, and the invasion success of pike, more populations from throughout pike's range should be examined. To alleviate these shortcomings and examine other potential founder populations, we

are currently expanding our work to include more populations from the native range in Alaska and from neighboring areas within North America (e.g., Ontario).

Key findings of this work extend our knowledge of pike standing genetic diversity to populations from Alaska and document strong bottleneck effects in the pike populations in Southcentral Alaska. This is noteworthy because since introduction in the 1950s, pike have continued to expand and have been implicated in the extirpation and declines of native fishes (Haught and von Hippel 2011; Sepulveda et al. 2013; Dunker et al. 2018). Apparently, the lack of diversity does not affect their invasion success as northern pike have continued their expansion into Southcentral Alaska. Although it is unclear whether introduced northern pike populations have locally adapted to conditions in their new areas, our finding suggests that genetic diversity is not a requisite condition of successful invasion. We were surprised to find that pike on the Kenai Peninsula exhibited higher genetic diversity than pike in the Susitna basin, indicative of higher propagule pressure on the Kenai Peninsula consistent with multiple sources of founders. Our results support the working hypothesis that the Kenai Peninsula pike originated from multiple, albeit yet unidentified, founding sources (Robert Massengill, ADF&G, *personal communication*, 2017). Although we did not succeed in determining the source of the invasion into Southcentral Alaska, our work provided baseline data for managers to monitor and detect signs of new introductions of pike.

Acknowledgements

Funding for this research was provided by the U.S. Geological Service Northern Rocky Mountain Science Center and the Alaska Department of Fish and Game (ADF&G). We are grateful to Dr. Adam Sepulveda who helped secure funding, develop project ideas, and assisted with sampling efforts. We are appreciative to numerous Alaskan agencies and their staff for

collecting pike samples across the state, including: Alaska Cooperative Fish and Wildlife Research Unit, ADF&G, Alaska Salmon Program of the University of Washington, Cook Inlet Aquaculture Association, National Park Service, Tyonek Tribal Conservation District, University of Alaska Fairbanks, and University of Alaska Museum of the North. Thank you to all the staff at the University of Alaska Museum fish genetics lab for processing hundreds of samples and getting them ready for sequencing.

References

Andrews, S. 2010. FastQC: a quality control tool for high throughput sequence data. available online at: http://www.bioinformatics.babraham.ac.uk/projects/fastqc.

Carlson, S. M., C. J. Cunningham, and P. A. H. Westley. 2014. Evolutionary rescue in a changing world. Trends in Ecology and Evolution 29(9):521–530. Elsevier Ltd.

Chhatre, V. E., and K. J. Emerson. 2017. StrAuto: automation and parallelization of structure analysis. BMC Bioinformatics 18(1):1–5. BMC Bioinformatics.

Clavero, M., and E. Garciaberthou. 2005. Invasive species are a leading cause of animal extinctions. Trends in Ecology & Evolution 20(3):110–110.

Craig, J. F. 1996. Population dynamies, predation and role in the community. Pages 201–217 Pike: Biology and exploitation. Chapman & Hal, London.

Danecek, P., A. Auton, G. Abecasis, C. A. Albers, E. Banks, M. A. DePristo, R. E. Handsaker, G. Lunter, G. T. Marth, S. T. Sherry, G. McVean, and R. Durbin. 2011. The variant call format and vcftools. Bioinformatics 27(15):2156–2158.

Davis, M. A., M. K. Chew, R. J. Hobbs, A. E. Lugo, J. J. Ewel, G. J. Vermeij, J. H. Brown, M. L. Rosenzweig, M. R. Gardener, S. P. Carroll, K. Thompson, S. T. A. Pickett, J. C. Stromberg, P. Del Tredici, K. N. Suding, J. G. Ehrenfeld, J. Philip Grime, J. Mascaro, and J. C. Briggs. 2011. Don't judge species on their origins. Nature 474(7350):153–154.

Dunker, K. J., A. J. Sepulveda, R. L. Massengill, and D. S. Rutz. 2018. The northern pike, a prized native but disastrous invasive. Pages 356–398 *in* C. Skov and P. A. Nilsson, editors. Biology and Ecology of Pike, 1st edition. CRC Press, Boca Raton.

Earl, D. A., and B. M. vonHoldt. 2012. STRUCTURE harvester: a website and program for visualizing structure output and implementing the evanno method. Conservation Genetics Resources 4(2):359–361.

Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software structure: a simulation study. Molecular Ecology 14(8):2611–2620.

Ewels, P., M. Magnusson, S. Lundin, and M. Kaller. 2016. MultiQC: summarize analysis results for multiple tools and samples in a single report. Bioinformatics 32(19):3047–3048.

Farris, J. S. 1972. Estimating phylogenetic trees from distance matrices. The American Naturalist 106(951):645–668.

Gosselin, T. 2017. Radiator: radseq data exploration, manipulation and visualization using R.

Goudet, J. 2005. HIERFSTAT , a package for R to compute and test hierarchical f-statistics. Molecular Ecology Notes 2:184–186.

Hale, M. L., T. M. Burg, and T. E. Steeves. 2012. Sampling for microsatellite-based population genetic studies: 25 to 30 individuals per population is enough to accurately estimate allele frequencies. PLoS One 7(9):e45170.

Haught, S., and F. A. von Hippel. 2011. Invasive pike establishment in cook inlet basin lakes, Alaska: diet, native fish abundance and lake environment. Biological Invasions 13(9):2103–2114.

Inskip, P. D. 1982. Habitat suitability index models: northern pike. Washington, DC.

Jacobsen, B. H., M. M. Hansen, and V. Loeschcke. 2004. Microsatellite dna analysis of northern pike (*Esox lucius* L.) populations: insights into the genetic structure and demographic history of a genetically depauperate species. Biological Journal of the Linnean Society 84(1):91–101.

Johnson, B. M., R. Arlinghaus, and P. J. Martinez. 2009. Are we doing all we can to stem the tide of illegal fish stocking? Fisheries 38(8):389–394.

Jombart, T. 2008. Adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24(11):1403–1405.

Kinziger, A. P., R. J. Nakamoto, E. C. Anderson, and B. C. Harvey. 2011. Small founding number and low genetic diversity in an introduced species exhibiting limited invasion success (speckled dace, *Rhinichthys osculus*). Ecology and Evolution 1(1):73–84.

Kolbe, J. J., R. E. Glor, L. Rodríguez Schettino, A. C. Lara, A. Larson, and J. B. Losos. 2004. Genetic variation increases during biological invasion by a cuban lizard. Nature 431(7005):177–181.

Kopelman, N. M., J. Mayzel, M. Jakobsson, N. A. Rosenberg, and I. Mayrose. 2015. Clumpak: a program for identifying clustering modes and packaging population structure inferences across k. Molecular Ecology Resources 15(5):1179–1191.

Leung, B., D. M. Lodge, D. Finnoff, J. F. Shogren, M. A. Lewis, and G. Lamberti. 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proceedings of the Royal Society B: Biological Sciences 269(1508):2407–2413.

Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20(5):223–228.

McMahon, T. E., and D. H. Bennett. 1996. Walleye and northern pike: boost or bane to northwest fisheries? Fisheries 21(8):6–13.

Miller, L. M., and W. Senanan. 2003. A review of northern pike population genetics research and its implications for management. North American Journal of Fisheries Management 23(1):297–306.

Mooney, H. A., and E. E. Cleland. 2001. The evolutionary impact of invasive species. Proceedings of the National Academy of Sciences 98(10):5446–5451.

Morrow, J. E. 1980. The freshwater fishes of Alaska. Alaska Northwest Publishing Company, Anchorage.

Moyle, P. B., and R. A. Leidy. 1992. Loss of biodiversity in aquatic ecosystems: evidence from fish faunas. Pages 127–169 *in* P. L. Fiedler and S. K. Jain, editors. Conservation Biology The Theory and Practice of Nature Conservation and Management, 1st edition. Chapman and Hall, New York and London.

Muhlfeld, C. C., S. T. Kalinowski, T. E. McMahon, M. L. Taper, S. Painter, R. F. Leary, and F. W. Allendorf. 2009. Hybridization rapidly reduces fitness of a native trout in the wild. Biology Letters 5(3):328–331.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89:583–590.

Nei, M., and W.-H. Li. 1979. Mathematical model for studying genetic variation in terms of restriction endonucleases. Proceedings of the National Academy of Sciences 76(10):5269–5273.

Peterson, B. K., J. N. Weber, E. H. Kay, H. S. Fisher, and H. E. Hoekstra. 2012. Double digest RADseq: an inexpensive method for de novo snp discovery and genotyping in model and non-model species. PLoS One 7(5):e37135.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the united states. Ecological Economics 52(3):273–288.

Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155(2):945–959.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raat, A. J. P. 1988. Synopsis of biological data on the northern pike *Esox lucius* Linnaeus, 1758. Rome.

Ricciardi, A., and H. J. Macisaac. 2010. Impacts of biological invasions on freshwater ecosystems. Pages 211–224 *in* D. M. Richardson, editor. Fifty Years of Invasion Ecology.

Rondeau, E. B., D. R. Minkley, J. S. Leong, A. M. Messmer, J. R. Jantzen, K. R. von Schalburg, C. Lemon, N. H. Bird, and B. F. Koop. 2014. The genome and linkage map of the northern pike (*Esox lucius*): conserved synteny revealed between the salmonid sister group and the neoteleostei. PLoS One 9(7):e102089.

Rosenberg, N. A. 2004. DISTRUCT: a program for the graphical display of population structure. Molecular Ecology Notes 4(1):137–138.

Saitou, N., and M. Nei. 1987. The neighbor-joining method - a new method for reconstructing phylogenetic trees. Molecular Biology and Evolution 4(4):406–425.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. Mccauley, P. O. Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive specie source: annual review of ecology and systematics. Annual Reviews Stable 32:305–332.

Schwoerer, T. 2017. Invasive elodea threatens remote ecosystem services in Alaska: a spatially-explicit bioeconomic risk analysis. University of Alaska Fairbanks.

Seeb, J. E., L. W. Seeb, D. W. Oates, and F. M. Utter. 1987. Genetic variation and postglacial dispersal of populations of northern pike (*Esox lucius*) in North America. Canadian Journal of Fisheries and Aquatic Sciences 44(3):556–561.

Sepulveda, A. J., D. S. Rutz, S. S. Ivey, K. J. Dunker, and J. A. Gross. 2013. Introduced northern pike predation on salmonids in southcentral Alaska. Ecology of Freshwater Fish 22(2):268–279.

Seutin, G., B. N. White, and P. T. Boag. 1991. Preservation of avian blood and tissue samples for dna analyses. Canadian Journal of Zoology 69(1):82–90.

Skog, A., L. A. Vøllestad, N. C. Stenseth, A. Kasumyan, and K. S. Jakobsen. 2014. Circumpolar phylogeography of the northern pike (*Esox lucius*) and its relationship to the amur pike (*E. reichertii*). Frontiers in Zoology 11(1):67.

Skov, C., M. C. Lucas, and L. Jacobsen. 2018. Spatial ecology. Pages 83–120 *in* C. Skov and P. A. Nilsson, editors. Biology and Ecology of Pike, 1st edition. CRC Press, Boca Raton.

Vitousek, P. M., C. M. DAntonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist 84(5):468–478.

Ward, R. D., M. Woodwark, and D. O. F. Skibinski. 1994. A comparison of genetic diversity levels in marine, freshwater, and anadromous fishes. Journal of Fish Biology 44(2):213–232.

Weir, B. S., and C. C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. Evolution 38(6):1358–1370.

Wennerström, L., D. Bekkevold, and L. Laikre. 2018. Population genetics of pike. Pages 164–184 *in* C. Skov and P. A. Nilsson, editors. Biology and Ecology of Pike, 1st edition. CRC Press, Boca Raton.

Westley, P. A. H. 2011. What invasive species reveal about the rate and form of contemporary phenotypic change in nature. Am Nat 177(4):496–509.

Willing, E. M., C. Dreyer, and C. van Oosterhout. 2012. Estimates of genetic differentiation measured by fst do not necessarily require large sample sizes when using many snp markers. PLoS One 7(8):e42649.

Wooller, M. J., B. Gaglioti, T. L. Fulton, A. Lopez, and B. Shapiro. 2015. Post-glacial dispersal patterns of northern pike inferred from an 8800 year old pike (*Esox cf. lucius*) skull from interior Alaska. Quaternary Science Reviews 120:118–125.

Yu, G., D. K. Smith, H. Zhu, Y. Guan, and T. T. Y. Lam. 2017. Ggtree: an R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. Methods in Ecology and Evolution 8(1):28–36.

Vander Zanden, M. J., J. D. Olden, J. H. Thorne, and N. E. Mandrak. 2004. Predicting occurrences and impacts of smallmouth bass introductions in north-temperate lakes. Ecological Applications 14(1):132–148.

Figures

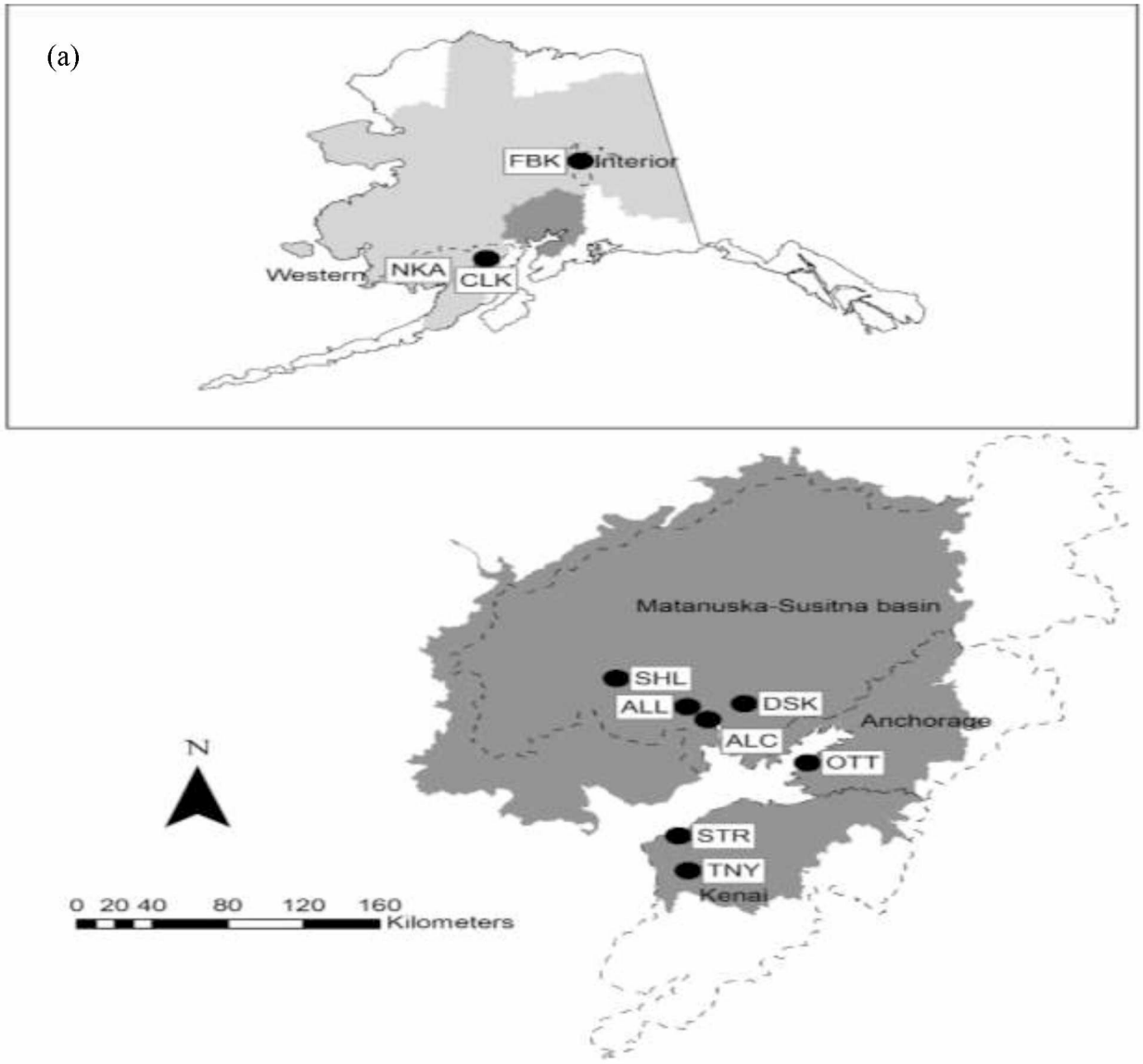


Figure 1.1. Northern pike sampling locations throughout Alaska with native sites shown in inset and invasive sites shown in main figure. Sampling locations are marked as circles. Inset (a) shows the distribution of native (light grey) and invasive (dark grey) northern pike in Alaska. Dashed outlines represent generalized areas corresponding to 'Area' in Table 1.1. Population definitions are located in Table 1.1.

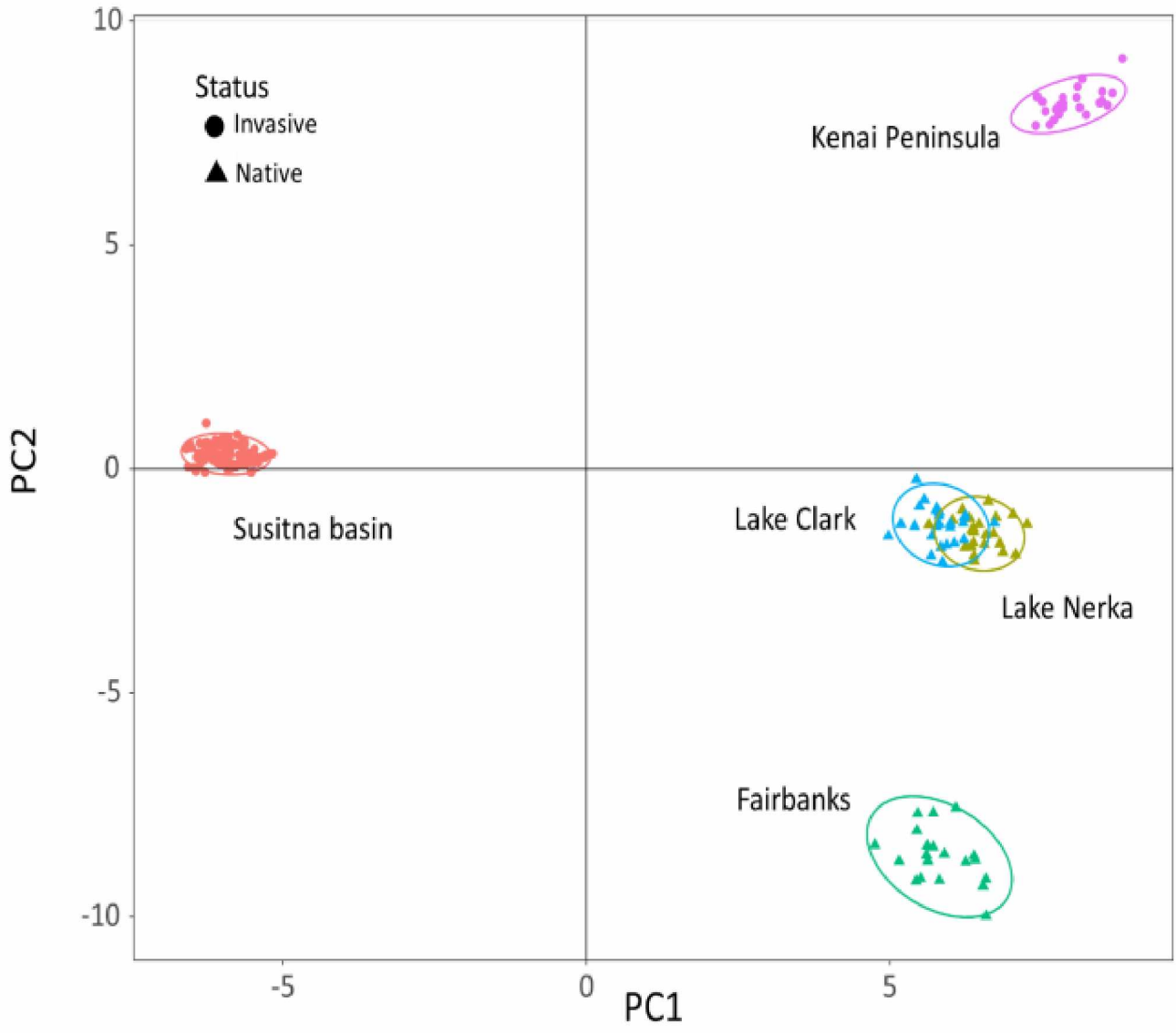


Figure 1.2. Discriminant Analysis of Principal Components of northern pike genetic diversity within Alaska, showing axes 1 and 2. Ellipses represent 95% confidence intervals. Invasive status is displayed as triangles for native populations and circles for introduced populations. Populations are grouped according to structure analysis (K = 5, see text for details).

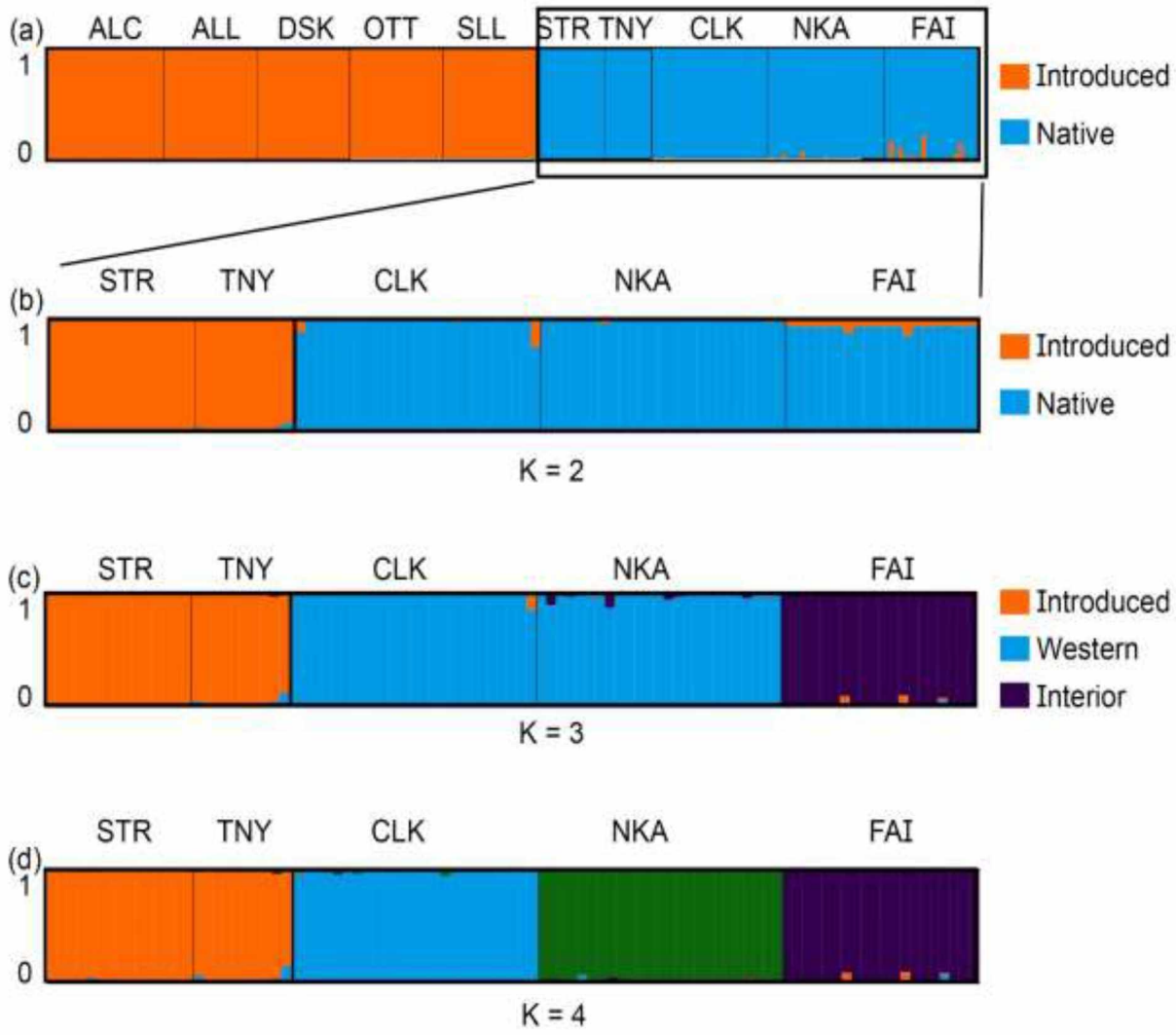


Figure 1.3. Hierarchical STRUCTURE results for introduced and native northern pike genetic structure. Individuals are represented by columns along the x-axis and the probability of group membership along the y-axis. Black rectangle represents populations shown in (b, c, d) with location as prior. See Table 1.1 for population definitions. (a) Divergence at K = 2 between native and introduced populations from the Susitna Basin. Note that STR and TNY are introduced but located on the Kenai Peninsula. (b – d) Structure of native and introduced Kenai Peninsula populations for K = 2, K = 3, and K =4. (c) Divergence of Western and Interior Alaska native populations.

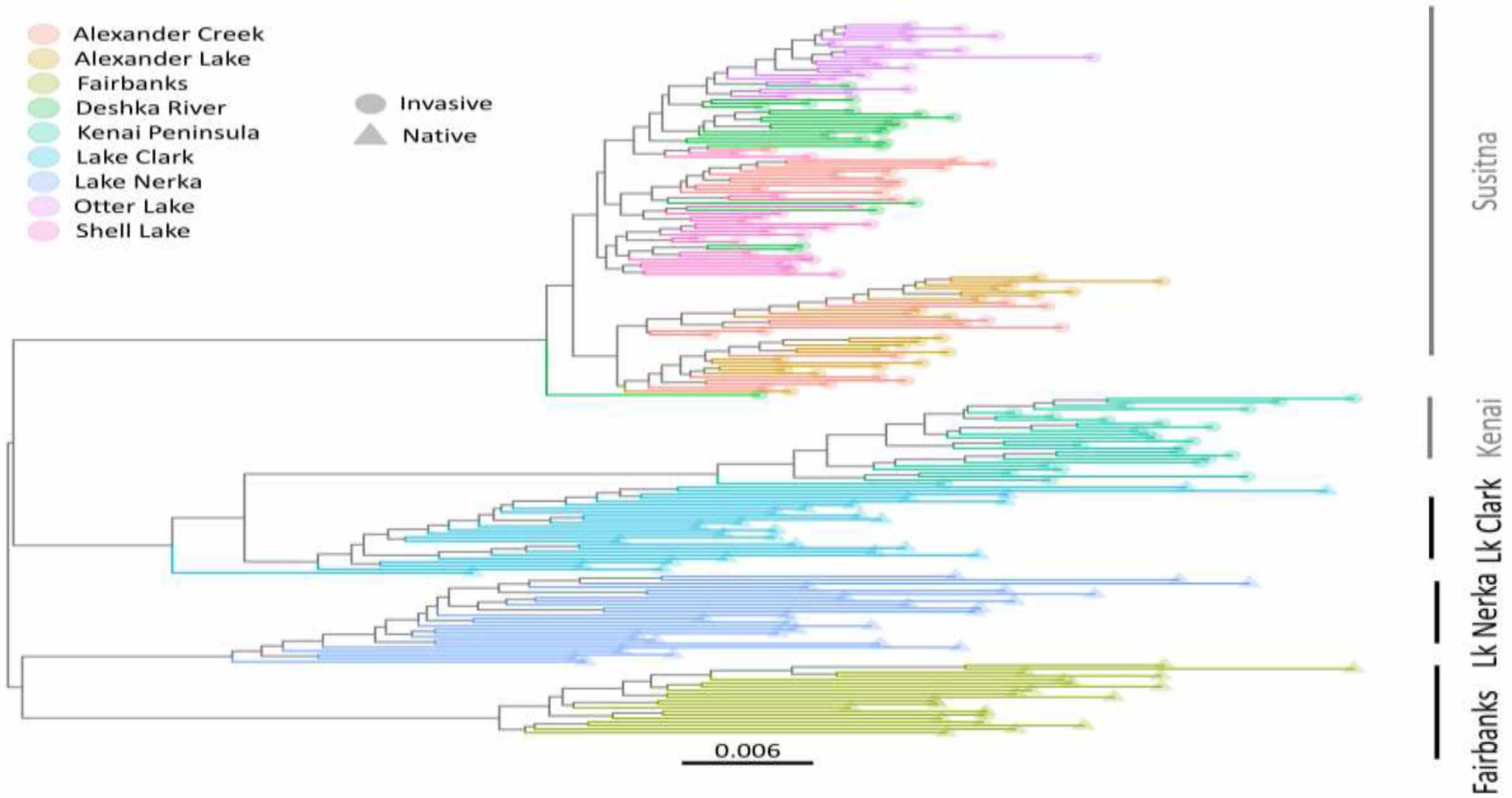


Figure 1.4. Midpoint rooted phylogenetic tree of native and invasive populations of northern pike in Alaska. Native populations are triangles and indicated by black. Invasive groups ("Kenai" and "Susitna"; see text for details) are circles and indicated by grey. The tree was created using neighbor-joining method and branch lengths were calculated using 100 bootstraps. There is no evidence of genetic structure in Susitna populations and invasive branches suggest alternate founding sources.

Tables

Table 1.1. Collection location, estimated year of invasion, and sample sizes for genotyped northern pike (*Esox lucius*) in Alaska, USA Collector agencies are as follows: ADFG, Alaska Department of Fish and Game; CIAA, Cook Inlet Aquaculture Association; UAF, University of Alaska Fairbanks; NPS, National Park Service.

Area	Location	Pop	Latitude	Longitude	Status	Est. invasion year	N	Collector
Susitna	Alexander Ck	ALC	61.637	-150.690	Invasive	1960	25	ADFG
Susitna	Alexander Lk	ALL	61.736	-150.887	Invasive	1970	20	ADFG
Susitna	Deshka R	DSK	61.745	-150.312	Invasive	1980	20	ADFG
Anchorage	Otter Lk	OTT	61.290	-149.738	Invasive	2000	20	ADFG
Susitna	Shell Lk	SHL	61.961	-151.581	Invasive	1980	20	CIAA
Kenai	Stormy Lk	STR	60.779	-151.065	Invasive	1970	15	ADFG
Kenai	Tiny Lk	TNY	60.520	-150.993	Invasive	unknown	10	ADFG
Interior	Fairbanks area	FBK	64.835	-147.784	Native	--	20	UAF
Western	Lk Clark	CLK	60.180	-154.562	Native	--	25	NPS
Western	Lk Nerka	NKA	59.547	-158.757	Native	--	25	UAF

Table 1.2. Estimates of genetic diversity across populations of pike throughout Alaska. Values shown are the mean for all positions, variable and fixed, in each population.

Pop	Pvt	N	% Poly	H_O	π
ALC	449	23.23	15.7	0.0258	0.000135
ALL	301	18.98	12.8	0.0205	0.00011
DSK	348	18.9	14.4	0.0231	0.000123
CLK	896	23.01	31.5	0.0491	0.000231
NKA	876	22.74	36	0.0549	0.000251
FBK	900	19.09	33.5	0.0510	0.000241
OTT	308	18.89	12.1	0.0153	0.0000845
SHL	291	19.42	12.6	0.0187	0.000101
STR	314	14.3	13.2	0.0273	0.000135
TNY	258	9.65	12.8	0.0283	0.00013
INV ALL	-	117.16	47	0.0227	0.000131
INV SUS	-	95.27	30.3	0.0207	--
INV KEN	-	23.71	18.8	0.0278	--
NAT	-	62.22	72.8	0.0360	0.000241

Pop = populations are as follows: ALC, Alexander Creek; ALL, Alexander Lake; DSK, Deshka River; CLK, Lake Clark; NKA, Lake Nerka; FBK, Fairbanks area; OTT, Otter Lake; SHL, Shell Lake; STR, Stormy Lake; TNY, Tiny Lake; INV ALL, all invasive; INV SUS, Susitna basin invasive; INV KEN, Kenai Peninsula invasive; NAT, all native.

Pvt, number of private alleles in the population; N, number of individuals per locus in the population; % Poly, percentage of polymorphic loci in the population; H_O, observed heterozygosity; π, mean nucleotide diversity

Table 1.3. Pairwise genetic difference (F_{ST}) among ten populations of northern pike around Alaska. F_{ST} is located above diagonal and 95% confidence intervals, based on 1,000 bootstrap replicates below diagonal. Estimates based on Weir and Cockerham's F_{ST} (1984). Population definitions are located in Table 1.1.

	ALC	ALL	FBK	DSK	CLK	NKA	OTT	SHL	STR	TNY
ALC	–	0.047	0.491	0.060	0.449	0.411	0.140	0.062	0.581	0.591
ALL	0.037, 0.058	–	0.515	0.164	0.482	0.432	0.273	0.164	0.625	0.638
FBK	0.469, 0.514	0.491, 0.538	–	0.488	0.376	0.339	0.532	0.511	0.505	0.502
DSK	0.049, 0.072	0.141, 0.19	0.466, 0.513	–	0.439	0.402	0.111	0.074	0.589	0.603
CLK	0.430, 0.472	0.464, 0.505	0.353, 0.401	0.420, 0.463	–	0.282	0.478	0.468	0.409	0.411
NKA	0.389, 0.430	0.411, 0.454	0.317, 0.36	0.377, 0.423	0.264, 0.302	–	0.439	0.422	0.377	0.372
OTT	0.123, 0.157	0.247, 0.303	0.511, 0.556	0.091, 0.130	0.457, 0.506	0.418, 0.464	–	0.136	0.636	0.668
SHL	0.051, 0.074	0.139, 0.195	0.488, 0.534	0.065, 0.086	0.448, 0.491	0.398, 0.445	0.113, 0.159	–	0.611	0.632
STR	0.552, 0.603	0.599, 0.644	0.484, 0.526	0.56, 0.612	0.385, 0.432	0.354, 0.408	0.607, 0.661	0.585, 0.634	–	0.161
TNY	0.557, 0.613	0.612, 0.656	0.483, 0.523	0.569, 0.625	0.388, 0.432	0.348, 0.397	0.642, 0.691	0.606, 0.655	0.144, 0.184	–

Appendices

Appendix 1.A. Filters applied by the *ipyrad* pipeline and number of loci lost at each stage.

	Total Filters	Applied Order	Retained Loci
Total Prefiltered Loci	52441	0	52441
Remove Duplicates	849	849	51592
Max Indels	815	815	50777
Max SNPs	589	14	50763
Max Shared Heterozygosity	300	248	50515
Min per Sample	34773	34242	16273
Max Alleles	1332	128	16145
Total Filtered Loci	16145	0	16145

Appendix 1.B. Measures of genetic diversity from other RAD-seq studies of fishes.

Authors	Species	π	H_E	H_O	F_{ST}	F_{IS}
Guo et al. 2015	*Gasterosteus aculeatus*	0.00358*	0.297	--	0.02825	--
Hillen et al 2017	*Dicentrarchus labrax*	--	0.201	0.205	0.221	0.026
Maroso et al. 2016	*Coryphaena hippurus*	--	0.255	0.254	0.0729	0.006
Siccha-Ramirez et al. 2018	*Thunnus albacares*	--	0.18	0.24	--	--
Siccha-Ramirez et al. 2018	*Scomberomorus brasiliensis*	--	0.24	--	--	--
Stobe et al. 2017	*Labeobarbus natalensis*	0.278 (0.0035)*	0.270 (0.0034)*	0.373 (0.0047)*	--	-0.218 (0.003)
Attard et al. 2017	*Macquaria ambigua*	--	0.244 - 0.281	0.222 - 0.326	0.024	-.089
Brauer et al. 2016	*Nannoperca australis*	--	0.161	0.123	0.3	--
Skovrind et al. 2016	*Leuciscus idus*	--	0.23	0.231	0.135 - 0.289[1] 0.001 - 0.047[2]	--
Black et al. 2017	*Cyprinodon bovinus*	--	0.29	0.301	0.062	--
Pérez-Portela et al. 2018[I]	*Pterois volitans*		0.256	0.241	0.116	0.273
Jalbert et al. 2018[I]	*Esox lucius*	0.00273	--	0.0326	0.424	--

Notes: * indicate author specified measurements taken from all SNPs, variable and fixed.

[I] indicate invasive species.

THIS PAGE INTENTIONALLY LEFT BLANK

Chapter 2: Vulnerability of Pacific salmon to invasion of northern pike (*Esox lucius*) in Southcentral Alaska[2]

Abstract

Worldwide invasion and range expansion of northern pike (*Esox lucius*) have been linked to the decline of native fishes and new techniques are needed to predict the vulnerability of habitats to invasion over broad geographic scales. We combined intrinsic potential habitat modeling with a Bayesian network to evaluate the vulnerability of five Pacific salmon species (*Oncorhynchus* spp.) to invasion by northern pike for 22 875 km of stream reaches in the Matanuska-Susitna basin, Alaska, USA. Pink salmon were the most vulnerable species, with 15.2% (2 458 km) of their known extent identified as "highly" vulnerable, followed closely by chum salmon (14.8%; 2 557 km) and coho salmon (14.7%; 2 536 km). We found 1 001 km of highly vulnerable streams that were shared by all five Pacific salmon species. Our framework is easy to implement, adaptable to any species or region, and cost effective. With increasing threats of species introductions, fishery managers need new tools like those described here to efficiently identify critical areas, especially when management resources are limited.

Introduction

Biological invasions are a leading cause of native biological diversity loss worldwide (Elton 1958, Moyle and Leidy 1992, Vitousek et al. 1996, Mooney and Cleland 2001). Increased reliance on freshwater systems for agriculture, hydropower, transportation, food, and recreation has led to the modification and simplification of river networks worldwide, increasing rates of disturbance and facilitating dispersal that often results in species range expansions (Vitousek et

[2] Jalbert, C.S., Falke, J.A., Westley, P.A.H, López, J.A., Dunker, K.J. and Sepulveda, A.J. 2018. Vulnerability of Pacific salmon to invasion of northern pike (*Esox lucius*) in Southcentral Alaska. Formatted for the Canadian Journal of Fisheries and Aquatic Sciences.

al. 1996, McKinney and Lockwood 1999). A subset of these introduced non-native species become invasive (sensu Davis et al. 2011) resulting in substantial environmental and economic impacts, with the latter estimated to amount to billions of US dollars per year (e.g., Eurasian Zebra Mussel, *Dreissena polymorpha*; Vitousek et al. 1996). In contrast, due to direct and indirect effects, the environmental costs caused by these invasions are difficult to quantify. As such, strategies to guide conservation efforts for native species and management of non-native species must be assessed across broad geographic extents (Vander Zanden et al. 2004, Vander Zanden and Olden 2008, Olden et al. 2011).

Vectors for species transport often include unintentional routes such as ballast water releases (Rahel 2007), and intentional methods like illegal introductions by humans to boost recreational hunting or fishing activity (Johnson et al. 2009). Although stocking fish can benefit anglers by increasing desired recreational fishing opportunities in an area, it can lead to detrimental consequences for native fauna including competition with other prized sportfish or extirpations of native fishes (Moyle and Light 1996b, Johnson et al. 2009). Illegal stocking has led to the rapid range expansion of numerous species resulting in a reduction in the diversity of freshwater fauna worldwide (Rahel 2002, 2007, Cambray 2003, Fausch and García-Berthou 2013). These intentional introductions can result in complex ecological consequences, even in relatively pristine ecosystems, especially when the invader is a top predator (Moyle and Light 1996a).

Worldwide invasion and range expansion of the highly predatory northern pike (*Esox lucius*; hereafter referred to as pike) have been increasing (McMahon and Bennett 1996, Johnson et al. 2009). In Alaska, pike are an ecologically and culturally important native fish species north and west of the Alaska Mountain Range, but do not naturally occur south of the range with the

exception of what is thought to be a post-glacial relict population near Yakutat, Alaska (Morrow 1980). In the 1950s, a floatplane pilot purportedly translocated pike from a native population in Minto Flats (65.00384, -149.20029) to Bulchitna Lake in the Susitna River basin with the intention of holding pike fishing derbies (Bulchitna Lake residents, personal communication, 2017). A small dam at the outlet of Bulchitna Lake was constructed to contain pike within the lake, but the occurrence of pike throughout Southcentral Alaska suggests that containment failed or that introductions were common and widespread (Figure S1). This illegal stocking event is thought to be the initial source of pike in the 60 000 km^2 Matanuska-Susitna basin (Haught and von Hippel 2011, Dunker et al. 2018). Additional illegal stocking events occurred in the 1960s into Alexander Lake (Susitna, Alaska, USA) as well as in lakes on Alaska's Kenai Peninsula (1970s), resulting in further establishment of pike populations (Dunker et al. 2018). Despite widespread concern about the impacts of pike, particularly on native Pacific salmon, little is known about invasive pike in Alaska (but see Patankar et al. 2006, Haught and von Hippel 2011, Sepulveda et al. 2013, 2015, Dunker 2014, Dunker et al. 2016, 2018). These studies have focused on diet, extirpation of native species, or eradication within single waterbodies (lakes or rivers), but a broad-scale assessment of current and future impacts of pike across Southcentral Alaska has not been conducted.

In Alaska, the invasion of pike has been linked to the rapid decline of multiple salmonid (salmon and trout) species (Rutz 1999, Dunker et al. 2018) as well as the extirpation of a rare weakly-armored threespine stickleback (*Gasterosteus aculeatus*) ecotype in Prator Lake, Alaska (Patankar et al. 2006; Rutz 1996; 1999; Sepulveda et al. 2015; 2013). Extirpation of species by introduced piscivores can be due to naivety of the prey to a novel predator (Sih et al. 2010) in habitats that lack sufficient habitat refugia. Since fish populations in Southcentral Alaska were

founded by colonizers following the end of the last glacial epoch, these communities have existed for approximately 10 000 years without pike. Thus, extirpations are likely to continue as pike spread throughout the invaded Matanuska-Susitna basin. Pike require slow moving, shallow, well-vegetated aquatic habitats to complete their life cycle and rely on vegetation for embryo and larval development (Casselman and Lewis 1996, Jacobsen and Engström-Öst 2018). This habitat type, common to Southcentral Alaska, also plays a key role in the life cycle of juvenile salmon (Bjornn and Reiser 1991). Diet analyses have identified juvenile salmon as the preferred prey of pike in their invaded range (Rutz 1999, Sepulveda et al. 2013, 2015) due to pike's preference for soft-rayed fishes (Eklöv et al. 1989) and their overlapping habitat use with juvenile salmon (Dunker et al. 2018). Thus, determining the extent to which salmon and pike may overlap is crucial for predicting the future impacts of the invasion and informing management decisions given the scale of the landscape and limited resources.

Substantial work to suppress or eradicate pike by the Alaska Department of Fish and Game (ADFG) has been completed or is underway to combat declining salmon populations in Southcentral Alaska. Estimated costs of the program were approximately $5 million for the period between 2008 and 2018, and to date pike have been successfully removed from 22 water bodies in the Anchorage, Yakutat, and Kenai areas where the species was present as a result of illegal stocking followed by dispersal throughout open systems (Dunker et al. 2018). With current management strategies, eradication of pike is unlikely to be achieved from all waterbodies in the Matanuska-Susitna basin, which spans an area approximately the size of Indiana, USA, due to abundant and highly-connected habitats and the remote nature of the system. Owing to limited resources, new tools are needed to allow triage of this invaded system

and prioritize areas on the landscape where threats to native populations from invasive pike are greatest.

The specific goal of this study was to provide the first assessment of the vulnerability of five Pacific salmon species (Chinook, *Oncorhynchus tshawytscha*; chum, *O. keta*; coho, *O. kisutch*; pink *O. gorbuscha*; and sockeye, *O. nerka*) to the ongoing invasion of pike in Southcentral Alaska, with the ultimate aim of guiding conservation prioritization efforts. Across the invaded and potentially invaded range of the Matanuska-Susitna basin, our objectives were to: 1) estimate the location, quantity, and potential of suitable pike habitat, 2) assess the overlap of high potential juvenile salmon and pike habitat using habitat suitability models, 3) quantify natural and human-mediated colonization throughout the stream network, and 4) combine these factors into a Bayesian network to estimate the vulnerability of each salmon species to pike invasion.

Materials and methods

Study area

The Matanuska-Susitna basin covers approximately 63 000 km^2 in Southcentral Alaska and is composed of two major watersheds, the Matanuska and the Susitna, that drain major portions of the southern Alaska Range mountains (Figure 1). Formed though glacial processes, the basin is surrounded by mountains, with the Alaska Mountain Range to the north, the Chugach and Talkeetna Mountains to the east, the Aleutian Mountain Range to the west, and Cook Inlet to the south. The riverine landscape is predominantly lowlands and contains thousands of lakes and ponds and over 38 000 km of streams and rivers draining into Cook Inlet. This complex habitat supports a diversity of native fishes, including: Chinook salmon, chum salmon, coho salmon, pink salmon, and sockeye salmon, rainbow trout and steelhead (*O.*

mykiss), Arctic grayling (*Thymallus arcticus*), dolly varden (*Salvelinus malma*), burbot (*Lota lota*), eulachon (*Thaleichthys pacificus*), longnose sucker (*Catostomus catostomus*), threespine (*Gasterosteus aculeatus*) and ninespine (*Pungitius puntitius*) stickleback, multiple whitefish (*Coregonus* spp. and *Prosopium* spp.), lamprey (*Lethenteron* spp. and *Entosphenus* spp.), and sculpin (*Cottus* spp.) species. Introduced in the 1950s, pike and Alaska blackfish (*Dallia pectoralis*) are also found throughout waterbodies of the Matanuska-Susitna basin (Kirsch et al. 2014).

Model of Pacific salmon vulnerability

We used a Bayesian network approach to assess the vulnerability of the five Pacific salmon species to invasion by pike in the Matanuska-Susitna basin, Alaska. Bayesian networks provide formal decision support for natural resource issues, and frequently incorporate habitat suitability models (Peterson et al. 2008, Falke et al. 2015) and climate scenarios (Peterson et al. 2013), to provide quantitative solutions to ecological problems (see McCann et al. 2006 for summary). Bayesian networks allow for the integration of qualitative and quantitative information from various sources and the prediction of outcomes for different scenarios (Marcot et al. 2006). They track uncertainty through each stage of the network and are easily modified to incorporate new information or data as they become available (Uusitalo 2007). These factors make Bayesian networks a useful tool with which to assess the vulnerability of ongoing invasions, as new information is regularly available, and management decisions often require multiple types and sources of data.

Three main variables (nodes) were included in the quantification of vulnerability within our Bayesian network: natural colonization, human-mediated colonization, and habitat overlap. As a first step, arrows representing cause and effect relationships were drawn between related

nodes, and probability tables representing the response of the node were created (Figure 2). Attributes contributing to these nodes were calculated as described below. A conditional probability table was created for each major node within the Bayesian network (Appendix B – D). The conditional probability tables quantify the response and uncertainty from parent nodes to each child node and were populated by examining published and unpublished data and utilizing expert opinion. We used Netica version 6.04 (Norsys Software Corp. 2017) to create and visualize the Bayesian network and conditional probability tables with node names, definitions, and states shown in Appendix E. All input nodes and their associated conditional probabilities, except the Pacific salmon intrinsic habitat potential node, remained constant among salmon species.

All statistical analyses were performed using the programs R version 3.5.0 (R Core Team 2017) and Netica version 6.04 (Norsys Software Corp. 2017). Spatial analyses were completed with R and ArcMap 10.4 (Environmental Systems Research Institute 2015, Redlands, California). All custom python scripts, R scripts, and ArcMap toolboxes are available upon request.

Model components

Our Bayesian network consisted of four components, which we discuss in detail below: the stream network, habitat potential within the stream network, natural colonization by pike, and human-mediated colonization by pike.

Stream network

Stream attributes were derived using a NetMap synthetic stream network which was created through a combination of 1 m IfSAR (interferometric synthetic aperture radar) and 5 m LiDAR (light detection and ranging) digital elevation models (DEMs) throughout the

Matanuska-Susitna basin (Benda et al. 2007). Clarke et al. (2008) describe the procedure used for generating NetMap stream attributes using flow accumulation and channel delineation algorithms. The NetMap stream network consisted of ca. 100 m (mean = 98.7 m ± 11.5 m [SD]) long stream reaches attributed with geomorphic characteristics (e.g., gradient, reach width, floodplain width, drainage area, etc.).

The final Matanuska-Susitna basin stream network extent used in our analyses consisted of 22 875 km of streams with upstream area > 5 km^2. The study area contained low-gradient reaches that averaged 0.029% (SD = 0.051%) and average elevation was 556 m (SD = 416 m). The Matanuska-Susitna basin contained 18 719 lakes with an average area of 0.0447 km^2 (SD = 0.840 km^2). On average, lakes had a maximum length of 236 m (SD = 420 m) and a fetch (see below for calculation) of 216 m (SD = 326 m).

Vulnerability of Pacific salmon

Habitat potential

Due to the difficulty of characterizing fish habitat quality at the stream reach-scale (10^2 – 10^3 m) over large portions of the landscape, habitat suitability models based on stream geomorphology, termed intrinsic potential models (IP; Burnett et al. 2007), have been developed to provide estimates of potential habitat for a species. Intrinsic potential models have been used to predict the distribution of salmonid habitat in the Pacific Northwest region of the conterminous U.S. and Alaska (Burnett et al. 2007, Bidlack et al. 2014, Matter et al. 2018). Generally, IP models use static (over ecological time scales), reach-scale, geomorphic attributes (e.g., channel confinement, gradient, floodplain width) to assign a suitability value for a species (Burnett et al. 2007). Suitability values are generated based on previous knowledge of the organism's habitat preferences and requirements. Intrinsic potential models can be generated for

different life stages (Agrawal et al. 2005, Shallin Busch et al. 2013), allowing for a greater understanding of the impacts of predation on juveniles or sensitivity to habitat alteration on adults (Burnett et al. 2007).

We used an intrinsic potential (IP; Burnett et al. 2007) approach to rank and estimate the distribution of habitat potential for each of the five Pacific salmon species and pike across the Matanuska-Susitna basin and to identify sites likely to provide habitat for salmon and pike and assess among-species habitat overlap. Habitat suitability for inclusion into the IP model was assigned on a scale of zero to one, with zero representing unsuitable and one representing fully-suitable habitat. Burnett et al. (2007) recommend three attributes for calculating the IP score of a reach as optimal. Generally, suitability scores are assigned based on expert opinion or empirical data for a given attribute value. The overall IP score is calculated as the geometric mean of the reach-specific suitability rankings for each of the selected attributes using

(1) $$IP_i = \sqrt[3]{x1_i * x2_i * x3_i}$$

where, x1, x2, x3 represent suitability rankings for three attributes in stream reach *i*.

The geometric mean is used to allow the least suitable attribute to carry the most overall weight in determining habitat suitability, thus zero values for any attribute will cause the overall IP to equal zero (i.e., low or no habitat potential). In the following section, we provide a detailed description of our specific IP calculations for Pacific salmon and pike in the Matanuska-Susitna basin. For all IP model development, we relied on previously identified fish-attribute relationships (salmon: Bidlack et al. 2014, Woll 2015, Romey 2018; pike: Inskip 1982, Raat 1988, Kirsch et al. 2014; R. Shaftel, Alaska Center for Conservation Science, unpublished data, 2017) or expert opinion when empirical data were not available.

Northern pike

We created IP models for pike in the Matanuska-Susitna basin based on expert opinion and by examining previously established relationships from the literature between pike presence and landscape attributes in their native range. We selected three attributes, gradient (% GRAD), elevation (ELEV_M), and floodplain width (FP_WIDTH; Figure 3), previously identified as important predictors of pike in their native range to build the IP (Kirsch et al. 2014; R. Shaftel, unpublished data, 2017).

Inskip (1982) hypothesized the relationship between pike and gradient for use in habitat suitability models. Generally, pike require standing or slow-moving water, thus high gradient streams characterized by faster flowing waters are thought to be unsuitable for pike. Moreover, gradient likely acts as a physical barrier for pike and limits their natural movement into upstream reaches (Inskip 1982). Our index curve assumes high habitat potential (suitability = 1) in areas of low gradient and little to no suitability for reaches with gradients $\geq$ 0.5 % (Figure 3a). Elevation (meters above sea level) is an important predictor of pike presence in the Matanuska-Susitna (Kirsch et al. 2014) and the Yukon-Kuskokwim (Southwest Alaska; R. Shaftel, unpublished data, 2017) areas. Further, elevation often serves as a proxy for many other factors known to influence the distribution of fish (e.g., climate, vegetation, water chemistry (Schmitt et al. 1993, Shallin Busch et al. 2013).We parameterized an index curve using data from previous studies and expert opinion. Our curve assumes high habitat potential for low elevation reaches (suitability = 1, 0 – 200 m) and no habitat potential for reaches greater than 200 m elevation (Figure 3b). Finally, floodplain width (m) was selected because larger floodplains provide more complex off-channel habitat which is necessary for adult and juvenile pike, and likely serves as a proxy for the presence of aquatic vegetation that is required for the pike life cycle (Crossman 1991, Casselman

and Lewis 1996, Dunker et al. 2018). The index curve for floodplain width classifies constrained reaches (< 50 m) as low suitability and reaches with large floodplains (> 500 m) highly suitable for pike (Figure 3c). We used the previously discussed attributes to calculate final IP scores (Equation 1) for stream reaches in the Matanuska-Susitna basin using the NetMap tools extension (Benda et al. 2007) for ArcGIS.

Juvenile Pacific salmon

We modified existing juvenile Pacific salmon rearing habitat IP models and applied the results to the Matanuska-Susitna basin study area to assess potential for overlap between juvenile Pacific salmon rearing habitat areas and pike. Here, salmon rearing habitat is defined as the freshwater habitat in which juvenile salmon have adequate food, shelter, and water conditions to survive and grow. Woll (2015) created habitat suitability models for coho salmon and sockeye salmon by examining previous studies, collecting empirical data, and through expert opinion. Custom python scripts (ArcPy for ArcGIS), provided by Woll (2015), for calculating stream attributes and salmon habitat suitability were modified for compatibility with the NetMap synthetic stream network and to more closely follow the IP methodology utilized for the other species. Specifically, since we were interested in the total habitat potential across our entire study extent, references to known barriers to fish passage and known species distribution data, based off the State of Alaska Anadromous Waters Catalog (AWC; Alaska Department of Fish and Game 2008) were removed from calculations. Romey (2018) created IP models for pink salmon and chum salmon in southeast Alaska, for inclusion in the NetMap toolset (versions > 3.1.6). We applied this model to the Matanuska-Susitna datasets without modification. Finally, an IP model for Chinook salmon in the Copper River watershed (Southcentral Alaska; Bidlack et al. 2014) was applied to the Matanuska-Susitna basin. Attributes included in the model were mean annual

flow ($m^3 \cdot s^{-1}$), gradient ($m \cdot m^{-1}$), and glacial area (% coverage). Mean annual flow and gradient were attributes from the NetMap dataset. We calculated the proportion of watershed glacial coverage upstream of each focal stream reach by selecting all glaciers from the NHDWaterbody layer (United States Geological Survey 2004) and using the upstream proportion tool found in the NetMap toolset extension for ArcGIS.

Habitat overlaps

To examine the overlap between potential pike habitat and potential salmon rearing habitats, we assigned three classes (low, moderate, or high) of overlap using conditional probability tables within Netica (Appendix A). We assessed overlap between pike and salmon for the five Pacific salmon species separately. Finally, we determined the quantity and location of 'highly-vulnerable' habitat shared between all salmon species.

Natural colonization

Northern pike dispersal

Colonization of new waterbodies by pike was modeled as a function of the species' estimated dispersal abilities and barriers to movement. The ADF&G Northern Pike Waters Catalog version 5 (PWC; Alaska Department of Fish and Game 2018) lists all known vulnerable, probable, and invaded lakes in the Matanuska-Susitna basin. We selected all PWC lakes with known pike populations (Status = 'Known', or 'Suppression') that are connected to the stream network (Connectivity = '2','3','4','5'). Lakes with inconclusive status determinations ('probable', 'vulnerable', or 'unconfirmed') or that were classified as landlocked were not included in analyses. Since introduction, pike have dispersed and colonized throughout the stream network and are now established in at least 75 lakes (Alaska Department of Fish and Game 2018). Invaded lakes were considered putative source populations and the hydrologic

distance (km) from the closest source population to each stream reach was calculated using STARS version 2.0.6 (Peterson and Ver Hoef 2014) toolbox in ArcMap. These tools were used to create a landscape network (i.e., ESRI geodatabase used for storing spatial relationships) which was converted into a spatial stream network so in-stream distances from each stream reach to the nearest invaded lake could be calculated using R.

The *fishmove* (0.3-3) R package (Radinger and Wolter 2014) was used to fit a pike-specific leptokurtic dispersal kernel (Fraser et al. 2001), providing a probability of occurrence as a function of distance from source. Predictions were based on parameters from a multiple regression of four variables (Radinger and Wolter 2014): fish length, caudal fin aspect ratio, stream order, and time. The authors found these four explanatory variables were the most informative fish morphometry and river characteristics when explaining dispersal within a stream network. The morphometric variables, aspect ratio of caudal fin and fish length, have been linked to swimming ability with caudal fin shape thought to be an indicator of the mode of locomotion employed by the species (for discussion see Radinger and Wolter 2014). We set the average fork length to 450 mm which approximates the overall average length of many populations in the Matanuska-Susitna basin (Berghaus et al. in prep), time was set to 365 days, and caudal fin aspect ratio and stream order were calculated as per the defaults for pike (1.39 and 6^{th}, respectively). The default parameters utilized by *fishmove* (i.e., aspect ratio) were originally derived by (Pauly 1989) and later incorporated into fishbase.org (Froese and Pauly 2018).

Barriers

The Alaska Department of Fish and Game Fish Passage Inventory Database (FPID) was used to identify potential anthropogenic barriers to natural pike movement in the Matanuska-Susitna basin (Eisenman and Doherty 2014). Culverts identified as barriers to fish movement

were assumed to be barriers to natural colonization for pike (RGG ranking = "red"; FPID database, January 2018). Red culverts were used to limit the extent of the stream network when considering dispersal from a source. Specifically, if red culverts were located between a pike source population and a stream reach, the distance from source-to-reach for the upstream reaches was marked as state = 0, as natural colonization is unlikely to occur.

Human-mediated colonization

Floatplane

Human vectors were considered important to this analysis as they have been implicated in the movement of pike throughout the system (Dunker et al. 2018). Two major anthropogenic vectors of introduction within the Matanuska-Susitna basin were identified as movement by air and road. Schwoerer (2017) identified float planes as dispersal mechanisms for invasive plants within the region given the lack of road access on the westside of the Susitna River basin. A survey of float plane pilots in the Matanuska-Susitna basin classified the size of lakes that pilots of single-engine aircraft can utilize and common origins and destinations (Schwoerer 2017). The most prominent origin was Lake Hood (Anchorage, AK), initiating approximately 66 % of all Matanuska-Susitna bound flights. These data were used to identify the number and identity of lakes which were susceptible to introduction by air.

Lake fetch, or the maximum length of a waterbody over which wind can blow, was identified as crucial in determining pilots' ability to land on a given lake (Schwoerer 2017). Thus, fetch was calculated for 18 719 lakes within the Matanuska-Susitna basin. Due to the computational complexity of calculating fetch, a relationship between maximum lake length and lake fetch was derived and utilized as a proxy. Although not available for Alaska, the National Hydrography Database (NHDPlus Version 2) contains numerous lake metrics for 363 313 lakes

in the contiguous United States. These data were used to parameterize a simple linear regression between lake fetch and maximum lake length ($R^2 = 0.916$; $P < 0.001$)

(2) $F_i = 0.778 * L_i + 32.1097$

where F_i represents fetch of lake i and L_i represents the maximum length of lake i.

We calculated the maximum length of lakes (FType = 390; NetMap dataset) within the Matanuska-Susitna basin using the minimum bounding geography tool in ArcMap. The tool calculates the length and width of the smallest rectangle which fits around a lake polygon. We assumed the longest measure of the bounding rectangle to be representative of maximum lake length. Finally, we calculated lake fetch using the established relationship between maximum lake length and fetch (Equation 2), for all lakes. Float plane accessible lakes were identified and ranked according to the type of aircraft and minimum fetch of the destination (Appendix F). Lakes were ranked from one to five with the higher rankings being available to all previous ranks (i.e., lakes of rank two support two classes of aircraft). The Matanuska-Susitna basin dataset was split into unique 12-digit hydrologic unit codes (HUC; hereafter 'subwatershed'; United States Geological Survey 2013). After assigning each lake a plane ranking, we summed the ranks of all lakes within each subwatershed. Lakes residing along the boundary of multiple subwatersheds were counted towards the total for each subwatershed. Finally, we assigned the summed lake value to all reaches residing within the bounds of each subwatershed, using a spatial join in ArcMap. This provided an estimate of single-engine aircraft accessibility to reaches within each subwatershed.

Roads

Anthropogenic infrastructure such as boat launches or public waterbody access sites are commonly used to predict presence of invasive aquatic species (Johnson et al. 2001, 2008,

Vander Zanden and Olden 2008). We used distance from an individual stream reach (m) to the nearest road as a proxy because data on boat launches and access sites are not available for our study area. Waterbodies close to roads are more likely to contain invasive species as a result of human-mediated introductions than waterbodies located farther away (van Kleef et al. 2008, Kaufman et al. 2009, Kizuka et al. 2014). We identified 4 776 km of major roadways and trails, all of which serve as potential conduits of invasion or movement using the Matanuska-Susitna Borough Open Data Infrastructure Roads MSB layer (Matanuska-Susitna Borough 2018). We calculated the Euclidian distance from the closest point along each stream reach to the nearest road in ArcMap using the "near" tool.

We binned measurements of distance from each reach to the closest road into three categories, close (< 1 200 m), moderate (1 201 – 3 600 m), and far (>3 600 m; Table 1) to determine and assign input node probabilities for human-mediated colonization. We calculated the sum of plane accessible lakes within each subwatershed and grouped them into four categories (none: 0; low: 0 – 10; moderate: 11 – 20; high: > 20). The human-mediated colonization node consisted of three states (low, moderate, and high) which were calculated using a conditional probability table (Appendix D).

Species-specific vulnerability

We utilized the leptokurtic dispersal kernel established using *fishmove* and examined the location of known barriers to fish movement to calculate the probability of natural colonization. We grouped in-stream distances to the closest known pike source into three categories (close: < 1 000 m; moderate: 1 000 – 10 000 m; far: > 10 000 m), based off the calculated movement capabilities of pike. We classified stream reaches into two groups, whether they were located above (1) or below (0) known barriers to fish passage. Barriers to fish movement in the

Matanuska-Susitna basin were Devil's Canyon (62.826417, -149.36673) and red culverts as identified by the FPID. The natural colonization node consisted of four states (none, low, moderate, and high).

We assessed the probability of habitat overlap between pike and each salmon species by classifying habitat IP into three categories (low, moderate, high). Intrinsic potential for pike, Chinook salmon, chum salmon, and pink salmon were classified based on a continuous scale (low = 0 – 0.25; moderate = 0.25 – 0.75; high = 0.75 – 1). Coho salmon and sockeye salmon habitat suitability were classified based on a discrete scale (low = 0 – 1; moderate = 2 – 3; high = 4). We based the conditional probability table for habitat overlap on known relationships between salmon and pike, and expert opinion (Appendix B).

We assessed the final node in our Bayesian network, vulnerability to invasion by pike, separately for each of the five Pacific salmon species. Vulnerability was estimated as a function of the three major nodes (habitat overlap, natural colonization, and human-mediated colonization) and their input nodes. The output probability was classified into three states (low, moderate, or high) based on a weighted conditional probability table (Appendix E). We built the conditional probability table by assigning weights to the classes within the three major nodes, weighting both within and among nodes (Appendix G). We assumed habitat overlap to be most informative to vulnerability assessment, thus assigning the highest weights (low: 0; moderate: 50; high: 100). Natural colonization was weighted as roughly half of habitat overlap (none: 0; low: 5; moderate: 25; high: 50). Finally, human-mediated colonization was assigned a lower weight (low: 0; moderate: 5; high: 10) due to the presumed lower likelihood of human-mediated stocking events in the region.

We assigned final probabilities by summing the conditional probability table inputs and sorting numerically based on this rank. We assigned a "high" vulnerability probability to the conditional probability table input with the highest rank (160). Similarly, a "low" probability was assigned to the input with the lowest rank (0). Inputs with identical ranks were considered identical and given matching vulnerability probabilities. We used the midpoint of the ranks (80) as the inflection point for our vulnerability probabilities with conditional probability table inputs below this weighted towards low vulnerability and inputs above weighted towards high vulnerability. Finally, we projected the states from each major node onto the river network by exporting the terminal node and summed the total length (km) of stream reaches falling into each category (low, moderate, high) within each of the nodes: habitat overlap, human-mediated colonization, natural colonization, and vulnerability.

Model sensitivity

We performed a sensitivity analysis within Netica to determine the influence of input variables on each outcome variable in the model. The degree of sensitivity of one node to another was calculated using the mutual information (i.e., entropy reduction) method.

Results

Habitat potential

Northern pike

Intrinsic potential modelling estimated 6% (1 364 km) of the Matanuska-Susitna basin to be highly suitable for pike and 84% (1 146 km) of highly suitable pike habitats were located in the lower portion of the basin (subwatershed Yenta River and Lower Susitna River). We identified an additional 10% (1 858 km) of the Matanuska-Susitna basin as moderately suitable habitat with 78% of this residing in the two previously mentioned lower basin subwatersheds.

The remainder of the basin was predicted to have low habitat suitability for pike because the reaches were at higher elevations (mean = 655 m ± 387 m [SD]) and gradients (mean = 0.035% ± 0.055% [SD]) or had little floodplain area (mean = 197 m ± 378 m [SD]) (Figure 4).

Juvenile Pacific salmon

Consistent with distinct life history and habitat requirements, Pacific salmon habitat potential differed among species (Figure 4). Coho salmon was predicted to have access to the most high-potential habitat (7 904 km), followed closely by chum salmon (7 760 km) and pink salmon (7 585 km). Finally, we predicted 2 326 km of high-quality Chinook salmon habitat but only 22 km of high potential sockeye salmon habitat due to their reliance on lakes for rearing. Despite a seeming lack of high-quality habitat, we identified Chinook salmon as having the highest available moderate-quality (IP = 0.25 – 0.75) habitat (9 623 km), followed by pink salmon (5 379 km), coho salmon (4 267 km), chum salmon (3 857 km), and sockeye salmon (3 828 km).

Habitat overlaps

The probability of overlap between pike and salmon rearing habitat differed by species with coho salmon showing the greatest "high" habitat overlap with 3 555 km of stream reaches (21% of available habitat), falling within this class. Coho salmon were followed by chum salmon (3 450 km, 20%), pink salmon (3 085 km, 18%), Chinook salmon (1 980 km, 11%) and finally sockeye salmon (1 364 km, 8%). Chinook salmon had the highest "moderate" class with 7% of their available habitat (1 237 km) located in this class. All other species had relatively low levels of moderate overlap, with coho salmon, chum salmon, sockeye salmon, and pink salmon experiencing between 1% – 4%, respectively. Overall, most of the potential habitat, for all salmon species, was classified in the "low" probability of overlap class (78% - 89%). There was

little predicted habitat overlap upstream of barriers. Chum salmon, coho salmon, and pink salmon each demonstrated 107 km of "high" and "moderate" class habitat overlap. There were 95 km of Chinook salmon streams in these two classes and only 24 km of sockeye salmon streams.

Natural colonization

Northern pike dispersal and barriers to colonization

We identified 67 potential lakes that may serve as sources of pike colonists within the study area, one natural barrier (Devil's Canyon, Susitna, AK), and 137 artificial culvert barriers to fish passage. Of the stream reaches excluded by barriers, 200 km were identified as close (<1 km; natural colonization class = high) to a known pike source but were not likely to be naturally invaded. The leptokurtic dispersal kernel predicted a kernel probability of 16% for pike within the Matanuska-Susitna basin dispersing 1 km and a probability of 4.5% for pike dispersing 10 km, over a one-year period (365 d).

Overall, approximately 5 586 km (24 %) of the Matanuska-Susitna basin was identified as unavailable for natural colonization due to barriers. Pike do not appear to be limited by barriers as we identified 19 km (1.4 %) of high-quality and 88 km (4.7 %) of moderate-quality habitat located above known barriers. Pink salmon were the most range restricted with 2 792 km (37%) of high-quality habitat located upstream of known barriers. They were followed closely by coho salmon with 2 515 km (32%) and chum salmon with 2 326 km (30%) of high-quality habitat located upstream of known barriers. We predicted a relatively small amount of high-quality Chinook salmon habitat (305 km; 13%) above barriers but 4 058 km of moderate-quality habitat. Coho salmon, pink salmon, chum salmon, and sockeye salmon had much less moderate-quality habitat above barriers, ranging from 771 km – 1 740 km.

Human-mediated colonization

We found 2 334 km of streams within 1 200 m of major Matanuska-Susitna Borough roads (node class = close). There were 1 806 km of streams in the moderate node class for distance from roadway (1 200 – 3 600 m). The remaining 19 035 km were located farther than 3 601 m from the nearest road (node class = far). We identified 2 567 lakes meeting the minimum fetch criteria described earlier. Of these, 266 lakes were excluded, based on aircraft range, for the smallest aircraft type (rank 1). No other aircraft classes were range-limited to destinations within our study area. Lakes large enough to support aircraft had an average area of 0.266 km^2 (SD = 2.26 km^2), an average length of 810 m (SD = 922 m), and a fetch of 623 m (SD = 717 m).

Species-specific vulnerability

Chum salmon had the highest risk to invasion as measured by total stream kilometers in the "high vulnerability" class (2 557 km). They were followed closely by coho salmon and pink salmon with 2 534 km and 2 458 km and less so by Chinook salmon (1 661 km) and sockeye salmon (1 196 km). Most of the Pacific salmon highly vulnerable stream reaches were in the Yentna River and Lower Susitna River subwatersheds (78%; Figure 5, Table 2). There were 12 654 km of streams predicted to have moderate vulnerability to invasion with Chinook salmon predicted to have the highest (3 235 km; Appendix H). Chum salmon, coho salmon, and pink salmon showed similar effects with 2 557 km, 2 534 km, and 2 458 km, respectively. Again, sockeye salmon displayed the lowest vulnerability in the class with only 1 196 km of streams.

The mean uncertainty associated with invasion vulnerability across all reaches in the basin and for all Pacific salmon ranged from 0.28 to 0.84 (mean ± SD = 0.67 ± 0.07). We estimated uncertainty of vulnerability to invasion within Netica, as the standard deviation of the

expected value for the final vulnerability node in our Bayesian network, for each reach. Sockeye salmon showed the least uncertainty of all salmon (mean ± SD = 0.63 ± 0.05; Figure S5), followed by Chinook salmon with a mean uncertainty of 0.66 (0.06 [SD]; Figure S2). The mean uncertainty for chum salmon, coho salmon, and pink salmon was approximately 0.69 (0.06 [SD]; Figures S2, S4, S6). For all salmon species, much of the high uncertainty areas were located relatively low in the basin (i.e., Yentna River and Lower Susitna River subwatersheds) but there was also a high degree of uncertainty in the Matanuska sub-basin (Figures S2 – S6), indicating that the state assignment was uncertain. Thus, additional variables may be necessary to fully explain the vulnerability of salmon in the Matanuska sub-basin.

Overall, the Bayesian network identified pink salmon as the most vulnerable species with 15.2% of pink salmon extent ranked as high vulnerability (Figures 6, S5). Chum salmon and coho salmon were ranked similarly (14.8% and 14.7%, respectively; Figures 5, S3 – S4), followed by Chinook salmon with 10.8% of their range ranked as highly vulnerable (Figures 5, S2). Finally, sockeye salmon showed the lowest vulnerability in the high class with 8.2% labeled as highly vulnerable (Figures 5, S5). We found 1 001 km of streams that were identified as highly vulnerable for all five species of Pacific salmon (Figure 5, S7).

Sensitivity analysis

A network sensitivity analysis demonstrated that the Bayesian network performed as expected. In the Bayesian network, salmon vulnerability to invasion was most sensitive to habitat overlap (variance reduction = 0.1267), followed by natural colonization (0.0221), and human-mediated colonization nodes (0.0023), and their components (Table 1; Figure 2).

Discussion

Managing the impacts of on-going invasions is appropriately likened to triage medicine, where the need for interventions far exceed available resources (Sepulveda et al. 2012). Here we inform the spatial management of the northern pike invasion of Southcentral Alaska through a flexible modeling approach easily extended to other species that combines habitat suitability modeling, estimates of connectivity, and Bayesian networks to assess the vulnerability of five Pacific salmon species confronted with a novel top predator. Our approach has broad application outside of Alaska as pike have been introduced and deemed 'invasive' throughout much of their non-native distribution and are currently threatening the persistence of a variety of native fishes (Western United States: Flinders and Bonar 2008, Canada: Nicholson et al. 2015, Spain: Rincon et al. 1990, and elsewhere in the Mediterranean: Ribeiro and Leunda 2012). In the face of increasing freshwater invasions, assessments such as the current study provide managers with a quantitative method to quickly, and more economically, assess the impacts of species introductions over large geographic ranges.

Intrinsic potential

Intrinsic potential models proved useful in identifying (1) potential habitat for northern pike and (2) juvenile salmon rearing habitat potential over ca. 100 m stream reaches throughout the Matanuska-Susitna basin. Intrinsic potential models are based on the relationship between fish use and geomorphic attributes assumed to provide estimates of potential habitat for a given species. For our IP models, we chose a 0.75 threshold for "high" potential habitat but recognize that this is artificial and subjective, potentially leading to underestimates of habitat potential (Matter et al. 2018). However, we argue that narrow ranges for the "low" (0 – 0.25) and "high" (0.75 – 1.0) habitat potential classes captured true habitat potential, while the range of the

"moderate" class (0.25 – 0.75) represented the uncertainty in the fish-attribute associations. Given the decline of some species in Southcentral Alaska (e.g., Chinook salmon, coho salmon and sockeye salmon), we recognize and stress the importance of considering moderate habitat potential areas for future management actions.

Northern Pike

Our study indicates that there is a substantial amount of potential habitat yet unoccupied by pike within the Matanuska-Susitna basin (at minimum 1 000 km), consistent with the pattern of an ongoing invasion. We constructed IP models with three attributes which are important predictors of pike throughout their native range (Figure 3). The first attribute, gradient, serves as a proxy for the presence of low velocity habitats required for pike. Our approach assumes that invasive pike exhibit similar habitat requirements as their native counterparts, thus we relied on an established gradient suitability curve (Inskip 1982). We think this assumption is reasonable as we captured native and invasive pike in similar habitats. Furthermore, all 94 geo-referenced observations of pike in the Susitna basin (ADFG, unpublished data) fell within our gradient curve. The second attribute, floodplain width, represents a surrogate measure of connectivity of a stream reach to its floodplain. Access to a well-vegetated floodplain is crucial for juvenile pike rearing and adult spawning (Scott and Crossman 1973, Casselman and Lewis 1996, Jacobsen and Engström-Öst 2018). Indirect measurements of floodplain accessibility have been incorporated in pike habitat suitability models (e.g., Inskip 1982, percent pools and backwaters during summer, Inskip 1982; percent of lakes in the watershed, R. Shaftel, unpublished data; and wetland type, Mingelbier et al. 2008) but our model was the first to utilize reach-scale measurements. Finally, elevation is an important predictor of pike in Alaska (Kirsch et al. 2014; R. Shaftel, unpublished data) and is commonly used for predicting fish distributions (Jowett and

Richardson 1996, Dauwalter and Rahel 2008, Rose et al. 2016). Elevation may serve as a proxy for climactic and physio-chemical variables (e.g., temperature, water quality; Dauwalter and Rahel 2008, Jaramillo-Villa et al. 2010) or position in the stream continuum (Rose et al. 2016). Similar to gradient, we relied on elevation data from the native range of pike to parameterize our curve. However, this is not to say that invasive pike will never occur above our elevation (200 m) threshold. High-elevation introductions, due to human-assisted events, are possible but are unlikely to result in upstream establishment of pike.

As discussed previously, intrinsic potential is a useful tool for predicting habitat potential for other species, but this is the first use of IP for northern pike. Our model was constructed in an area with limited pike distribution data, so it was not possible to statistically verify our suitability curves. However, all 94 georeferenced observations of pike (ADFG, unpublished data) fell within our high-quality habitat class, providing some evidence that our curves performed adequately for predicting potential pike habitat.

Pacific salmon

Our assessment of salmon rearing habitat demonstrated a large quantity of potential habitat for all species and generally aligned with previously conducted suitability estimates for the region (Woll 2015). Our pink salmon and chum salmon IP models were created for streams in Southeast Alaska (Romey 2018) and care should be taken when applying IP models from outside the study area. That caveat notwithstanding, Matter et al. (2018) suggest that species- or life stage-specific IP models are robust outside the area they were parameterized for. Our analyses would benefit from further work ground-truthing pink salmon and chum salmon distribution in Southcentral Alaska. The Chinook salmon, coho salmon, and sockeye salmon IP models are specific to our study area (Woll 2015) but do not strictly follow the general format of

using three geomorphic attributes. We modified the models created by Woll (2015) by removing known salmon distribution limits, which we incorporated as barriers in our Bayesian network. Finally, we are unaware of sockeye salmon IP models, due to their complex life cycle with a reliance on lakes for rearing. We modified the habitat suitability model created by Woll (2015) by removing references to known sockeye lakes, as they were not included in our river network. Sockeye salmon in the Matanuska-Susitna basin can be exposed to heavy predation during the rearing period if pike are also present (Rutz 1996, 1999, Smukall 2015) and are highly vulnerable during seaward migrations as smolt if pike habitat is located downstream (i.e., near the outlet) of rearing lakes. Due to a limited IP model for sockeye salmon, the vulnerability estimates we produced are necessarily an underestimate of the vulnerability for this species. As such, we present the sockeye salmon results with caution and encourage further development of a lake-rearing sockeye salmon IP model.

Vulnerability assessment

Our vulnerability assessment provides a framework to identify hotspots along the stream network where fisheries managers can focus monitoring or eradication efforts. We identified critically vulnerable areas, shared by multiple salmon species, by calculating vulnerability across the entire stream network at fine scale (ca. 100 m reach), which can easily be scaled up (i.e., averaged or aggregated) to the watershed, sub-basin, or basin levels. This form of triage is crucial for managing invasions at a large scale as it provides the information necessary to gain the highest return on investment, while working with limited resources.

Estimates of human-mediated colonization by air were based on the relationship between minimum lake fetch and type of single-engine aircraft (Schwoerer 2017). We suspected aircraft range could be used to exclude lakes from our analyses but determined that only one class of

aircraft (Appendix F; Rank = 1) was range-limited in our study area. However, this class consisted of smaller aircraft which may originate from outside of our calculated origin (Lake Hood, Anchorage, Alaska). Limited data are available regarding illegal stocking of waterbodies as a function of distance to road or trail. However, lakes visible from roads have a higher incidence of establishment of non-native species (Kaufman et al. 2009, Kizuka et al. 2014), so we limited our high-class vulnerability to within 1 200 m from a road. Similarly, we limited the moderate class to a range of 1 200 – 3 600 m to account for introduction by all-terrain vehicles which are popular within the study area. That said, we acknowledge that distance to roads and potential for increased propagule pressure is likely confounded by other unquantified forms of disturbance (e.g., urbanization near lakes) that increase the likelihood of illegal introduction.

The dispersal ability of pike is a disputed topic with some studies agreeing with the "restricted movement paradigm" (Gerking 1959), regarding pike as a sedentary species, dispersing meters each day, yet other studies have found pike capable of dispersing up to 26 km d^{-1} (see Skov et al. 2018). Our estimates of natural colonization were calculated using a generalized leptokurtic dispersal kernel parameterized for pike and verified using radio telemetry data from pike in their native range (Fairbanks and Yukon, AK; ADFG, unpublished data). The telemetry data revealed that pike exhibit patterns of movement similar to many other species, with most of the population remaining sedentary and a few individuals demonstrating long distance dispersal. We limited our analyses to streams located below barriers to fish passage as identified by ADFG's Fish Passage Inventory Database (FPID; red culverts) and Devil's Canyon. The FPID ranks culverts based on their ability to allow for passage of juvenile coho salmon, which we assumed relevant for pike since they are weak swimmers and jumpers (Peake 2008). However, very little is known regarding pike jumping ability, so the potential to bypass

barriers is unknown. It is noteworthy that while there is potential for introduction above barriers, our pike IP model predicted a very small amount (106 km) of moderate or high potential habitat in reaches upstream of barriers in our study area. Thus, concerns of pike invasions due to culvert redesign or removal are not warranted.

Study limitations and uncertainties

Generally, uncertainty estimates within our Bayesian network are relatively high in the Yentna River, Lower Susitna River, and Matanuska River sub-basins. As most variables of the Bayesian network remained constant, changes in uncertainty here represent changes in habitat potential estimates, for each species, and their overlap with pike. Narrowing the range of our "moderate" habitat potential class (i.e., IP = 0.25 – 0.75) may lessen the uncertainty associated with the predictions. Also, future work validating and refining the pike and salmon IP models could allow for more accurate representation of the true habitat potential in the Matanuska-Susitna basin, which in turn would reduce the uncertainty associated with our vulnerability estimates.

Our vulnerability assessment does not directly consider life history differences among salmon species, particularly differences in the length of the freshwater rearing period during which anadromous salmon may be exposed to pike predation. Given this, pink salmon and chum salmon, which we identified as highly vulnerable based on habitat overlap, may be less affected because they migrate directly to sea upon emergence (Quinn 2005). Thus, depending on species life-history characteristics, the temporal overlap is minimized, and their vulnerability may be less than predicted. It seems logical that rearing is the most vulnerable salmon life-stage because most predation occurs on juveniles during most of their freshwater residency.

Our salmon IP models are specific to juvenile rearing habitat potential and do not consider outmigration, or the period in which juvenile salmon travel from freshwater to the ocean. This period of downstream movement has potential to expose juveniles to predation. However, the extent of predation is dependent on time spent in proximity to a predator, the number of predator's present, and prey density (Petersen and Deangelis 2000). Hence, a fine scale understanding of the relative spatial locations and movement patterns of the predator to the prey is crucial for accurately evaluating the extent of predator-prey interactions. Our IP models predict habitat potential over spatial scales (ca. 100 m reach) that do not allow for examination of such fine-scale patterns. For example, in the Matanuska-Susitna basin, as the prey (juvenile salmon) move downstream and into the mainstems of larger rivers, the predators (northern pike) are likely constrained to slower moving, off-channel habitats within those rivers. So, while a stream reach may exhibit high pike and salmon habitat potential, the two species may not overlap due to different microhabitat utilization. Further, many large rivers in the Matanuska-Susitna basin are glacial and highly turbid so as visual predators (Craig 2008), pike are likely at a disadvantage during the high-flow periods when smolt are out-migrating. More clearly, we argue that juvenile salmon can seek refuge from predation by moving into, traveling through, and rearing in habitat unsuitable for pike during their outmigration. Future work to investigate the frequency and duration at which pike move into sub-optimal habitats to pursue out-migrating smolt could inform this shortfall.

Management implications

The persistence and sustainability of Pacific salmon are vital to the preservation of economies, ecosystems, and cultures in Alaska. Repeat low returns and population-level declines of salmon in Southcentral Alaska led to emergency orders and pre-emptive closures of sport and

commercial Chinook salmon fisheries by ADF&G during recent fishing seasons. Our work, examining the overlap between potential habitat of pike and salmon, is a critical step in tying together pike research throughout the region and providing the tools to proactively respond to the invasion with the goal of mitigating the current and future impacts of non-native northern pike.

Since the invasion in the Matanuska-Susitna basin is widespread and we identified additional uncolonized potential habitat, we unfortunately predict the invasion will continue to expand. Faced with this realization, we believe that current eradication techniques are unlikely to result in the elimination of pike from the Matanuska-Susitna basin. Alaska Department of Fish and Game management techniques have been successful in suppressing or eliminating pike from certain areas such as closed lakes and smaller drainages, but suppression must be continued indefinitely. Moreover, managers must continually monitor the system for new invasions via natural and human-mediated colonization (Dunker et al. 2018). For example, Spens et al. (2007) found that given opportunity (time) pike colonized lakes in Sweden regardless of distance from source. Since the invasion in Southcentral Alaska is from a recent colonization, identifying all suitable habitat and habitat in which multiple salmon species are vulnerable will prove crucial in developing management plans to respond to the invasion.

Despite the potential limitations of our study, the invasion of pike within Southcentral Alaska presented us with an opportunity to apply flexible techniques to assess the vulnerability of multiple salmon species across the landscape. We demonstrated how tools like IP and Bayesian networks can be utilized to investigate the future of invasions, efficiently identify critical areas where management actions will attain the greatest benefits and be readily adapted for use with other species and areas. Finally, although we know that northern pike are not the sole or, in many cases, primary threat to Pacific salmon in Southcentral Alaska, our results

demonstrate a clear overlap between pike and salmon in this region. Specifically, as pike continue to invade suitable habitat, they are likely to interact with the Matanuska-Susitna basins naïve salmon and will further impact already struggling salmon returns.

Acknowledgements

This work was supported by the Alaska Department of Fish and Game and completed as partial fulfillment of a Master of Science degree in Fisheries at the University of Alaska Fairbanks. We thank Christine Woll (The Nature Conservancy) for providing insight and scripts used in prior work investigating intrinsic potential of Pacific salmon in the Matanuska-Susitna basin, and Kevin Andras and Lee Benda (TerrainWorks) for providing the NetMap platform and consistently addressing our bug reports by regularly providing software updates critical for successful completion of this study. Additionally, we thank the staff of the Alaska Department of Fish and Game Fish Passage Inventory Program for providing a database of all known barriers to fish passage in our study area. Finally, thanks to the staff of the Alaska Cooperative Fish and Wildlife Research Unit, and the College of Fisheries and Ocean Sciences for continued support throughout this project.

References

Agrawal, A., Schick, R.S., Bjorkstedt, E.P., Szerlong, R.G., Goslin, M.N., Spence, B.C., Williams, T.H., and Burnett, K.M. 2005. Predicting the potential for historical coho, Chinook and steelhead habitat in Northern California. NOAA Tech. Memo. (June): 25. doi:NOAA-TM-NMFS-SWFSC-379.

Alaska Department of Fish and Game. 2008. The Catalog of Waters Important for the Spawning, Rearing or Migration of Anadromous Fishes. Available from https://www.adfg.alaska.gov/sf/SARR/AWC/ [accessed 1 January 2018].

Alaska Department of Fish and Game. 2018. The Northern Pike Waters Catalog. Available from http://www.arcgis.com/home/webmap/viewer.html?url=https%3A%2F%2Fgis.adfg.alaska.gov%2Fags%2Frest%2Fservices%2Fsf_public%2FPikeWaters%2FMapServer&source=sd [accessed 1 January 2018].

Benda, L., Miller, D., Andras, K., Bigelow, P., Reeves, G.H., and Michael, D. 2007. NetMap: A new tool in support of watershed science and resource management. For. Sci. **53**(2): 206–219.

Berghaus, K., Spencer, J., and Westley, P.A.H. 2018. Contemporary phenotypic divergence of a renowned freshwater predator: Northern pike (*Esox lucius*) in its introduced and native ranges of Alaska. prep.

Bidlack, A.L., Benda, L.E., Miewald, T., Reeves, G.H., and McMahan, G. 2014. Identifying suitable habitat for Chinook salmon across a large, glaciated watershed. Trans. Am. Fish. Soc. **143**(3): 689–699. doi:10.1080/00028487.2014.880739.

Bjornn, T., and Reiser, D. 1991. Habitat requirements of salmonids in streams. *In* Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats. *Edited by* W.R. Meehan. American Fisheries Society Special Publication. pp. 83–138. Available from http://www.csa.com/partners/viewrecord.php?requester=gs&collection=ENV&recid=5445908.

Burnett, K.M., Reeves, G.H., Miller, D.J., Clarke, S., Vance-Borland, K., and Christiansen, K. 2007. Distribution of salmon-habitat potential relative to landscape characteristics and implications for conservation. Ecol Appl **17**(1): 66–80. Available from https://www.ncbi.nlm.nih.gov/pubmed/17479835.

Cambray, J.A. 2003. Impact on indigenous species biodiversity caused by the globalisation of alien recreational freshwater fisheries. Hydrobiologia **500**: 217–230. doi:10.1023/A:1024648719995.

Casselman, J.M., and Lewis, C.A. 1996. Habitat requirements of northern pike (*Esox lucius*). Can. J. Fish. Aquat. Sci. **53**(S1): 161–174. doi:10.1139/f96-019.

Clarke, S.E., Burnett, K.M., and Miller, D.J. 2008. Modeling streams and hydrogeomorphic attributes in Oregon from digital and field data. J. Am. Water Resour. Assoc. **44**(2): 459–477. doi:10.1111/j.1752-1688.2008.00175.x.

Craig, J.F. 2008. A short review of pike ecology. Hydrobiologia **601**(1): 5–16. doi:10.1007/s10750-007-9262-3.

Crossman, E.J. 1991. Introduced freshwater fishes: A Review of the North American Perspective With Emphasis on Canada. Can. J. Fish. Aquat. Sci. doi:10.1139/f91-303.

Dauwalter, D.C., and Rahel, F.J. 2008. Distribution modelling to guide stream fish conservation: an example using the mountain sucker in the Black Hills National Forest, USA. Aquat. Conserv. Mar. Freshw. Ecosyst. **18**(7): 1263–1276. doi:10.1002/aqc.940.

Davis, M.A., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J., Brown, J.H., Rosenzweig, M.L., Gardener, M.R., Carroll, S.P., Thompson, K., Pickett, S.T.A., Stromberg, J.C., Tredici, P. Del, Suding, K.N., Ehrenfeld, J.G., Philip Grime, J., Mascaro, J., and Briggs, J.C. 2011. Don't judge species on their origins. Nature **474**(7350): 153–154. doi:10.1038/474153a.

Dunker, K.J. 2014. Control and Eradication of Invasive Northern Pike in Southcentral Alaska.

Dunker, K.J., Sepulveda, A.J., Massengill, R.L., Olsen, J.B., Russ, O.L., Wenburg, J.K., and Antonovich, A. 2016. Potential of environmental DNA to evaluate Northern Pike (*Esox lucius*) eradication efforts: an experimental test and case study. PLoS One **11**(9): e0162277. doi:10.1371/journal.pone.0162277.

Dunker, K.J., Sepulveda, A.J., Massengill, R.L., and Rutz, D.S. 2018. The Northern Pike, a prized native but disastrous invasive. *In* Biology and Ecology of Pike, 1st edition. *Edited by* C. Skov and P.A. Nilsson. CRC Press, Boca Raton. pp. 356–398. Available from https://www.crcpress.com/Biology-and-Ecology-of-Pike/Skov-Nilsson/p/book/9781482262902.

Eisenman, M., and Doherty, G.M.O. 2014. Culvert inventory and assessment for fish passage in the State of Alaska: a guide to the procedures and techniques used to inventory and assess stream crossings. 2009-2014. *In* Special Publication No. 14-08. Anchorage.

Eklöv, P., Hamrin, S.F., and Eklov, P. 1989. Predatory Efficiency and Prey Selection: Interactions between Pike *Esox lucius*, Perch *Perca fluviatilis* and Rudd *Scardinus erythrophthalmus*. Oikos **56**(2): 149. doi:10.2307/3565330.

Elton, C.S. 1958. The ecology of invasions by animals and plants. Methuen & Co LTD, London.

Falke, J.A., Flitcroft, R.L., Dunham, J.B., McNyset, K.M., Hessburg, P.F., and Reeves, G.H. 2015. Climate change and vulnerability of bull trout (*Salvelinus confluentus*) in a fire-prone landscape. Can. J. Fish. Aquat. Sci. **72**(2): 304–318. doi:10.1139/cjfas-2014-0098.

Fausch, K.D., and García-Berthou, E. 2013. River conservation: challenges and opportunities. *In* The problem of invasive species in river ecosystems, 1st edition. *Edited by* S. Sabater and A. Elosegi. Fundación BBVA. pp. 193–215.

Flinders, J.M., and Bonar, S.A. 2008. Growth, condition, diet, and consumption rates of northern pike in three arizona reservoirs. Lake Reserv. Manag. **24**(2): 99–111. doi:10.1080/07438140809354054.

Fraser, D.F., Gilliam, J.F., Daley, M.J., Le, A.N., and Skalski, G.T. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. Am. Nat. **158**(2): 124–135. doi:10.1086/321307.

Froese, R., and Pauly, D. 2018. FishBase. Available from http://www.fishbase.org [accessed 12 January 2017].

Gerking, S.D. 1959. The restricted movement of fish populations. Biol. Rev. **34**: 221–242. doi:10.1111/j.1469-185X.1959.tb01289.x.

Haught, S., and von Hippel, F.A. 2011. Invasive pike establishment in Cook Inlet Basin lakes, Alaska: diet, native fish abundance and lake environment. Biol. Invasions **13**(9): 2103–2114. doi:10.1007/s10530-011-0029-4.

Inskip, P.D. 1982. Habitat suitability index models: Northern Pike. Washington, DC.

Jacobsen, L., and Engström-Öst, J. 2018. Coping with environments; vegetation, turbidity and abiotics. *In* Biology and Ecology of Pike, 1st edition. *Edited by* C. Skov and P.A. Nilsson. CRC, Boca Raton. pp. 32–61. Available from https://www.crcpress.com/Biology-and-Ecology-of-Pike/Skov-Nilsson/p/book/9781482262902.

Jaramillo-Villa, U., Maldonado-Ocampo, J.A., and Escobar, F. 2010. Altitudinal variation in fish assemblage diversity in streams of the central Andes of Colombia. J. Fish Biol. **76**(10): 2401–2417. doi:10.1111/j.1095-8649.2010.02629.x.

Johnson, B.M., Arlinghaus, R., and Martinez, P.J. 2009. Are we doing all we can to stem the tide of illegal fish stocking? Fisheries **38**(8): 389–394.

Johnson, L.E., Ricciardi, A., Carlton, J.T., Applications, E., and Dec, N. 2001. Overland dispersal of aquatic invasive species: a risk assessment of transient recreational boating. **11**(6): 1789–1799. doi:10.1890/1051-0761(2001)011[1789:ODOAIS]2.0.CO;2.

Johnson, P.T., Olden, J.D., and Vander Zanden, M.J. 2008. Dam invaders: impoundments facilitate biological invasions into freshwaters. Front. Ecol. Environ. **6**(7): 357–363. doi:10.1890/070156.

Jowett, I.G., and Richardson, J. 1996. Distribution and abundance of freshwater fish in New Zealand rivers. New Zeal. J. Mar. Freshw. Res. **30**(2): 239–255. doi:10.1080/00288330.1996.9516712.

Kaufman, S.D., Snucins, E., Gunn, J.M., and Selinger, W. 2009. Impacts of road access on lake trout (*Salvelinus namaycush*) populations: regional scale effects of overexploitation and the introduction of smallmouth bass (*Micropterus dolomieu*). Can. J. Fish. Aquat. Sci. **66**(2): 212–223. doi:10.1139/F08-205.

Kirsch, J.M., Buckwalter, J.D., and Reed, D.J. 2014. Fish inventory and anadromous cataloging in the Susitna River, Matanuska River, and Knik River basins, 2003 and 2011. Available from http://www.adfg.alaska.gov/FedAidpdfs/FDS14-04.

Kizuka, T., Akasaka, M., Kadoya, T., and Takamura, N. 2014. Visibility from roads predict the distribution of invasive fishes in agricultural ponds. PLoS One **9**(6): e99709. doi:10.1371/journal.pone.0099709.

Marcot, B.G., Steventon, J.D., Sutherland, G.D., and McCann, R.K. 2006. Guidelines for developing and updating Bayesian Belief Networks applied to ecological modeling and conservation. Can. J. For. Res. **36**(12): 3063–3074. doi:10.1139/x06-135.

Matanuska-Susitna Borough. 2018. Infrastructure Roads MSB | Matanuska-Susitna Borough Open Data. Available from https://data1-msb.opendata.arcgis.com/datasets/infrastructure-roads-msb [accessed 7 June 2018].

Matter, A.N., Falke, J.A., López, J.A., and Savereide, J.W. 2018. A rapid-assessment method to estimate the distribution of juvenile Chinook salmon in tributary habitats using eDNA and occupancy estimation. North Am. J. Fish. Manag. **38**(1): 223–236. doi:10.1002/nafm.10014.

McCann, R.K., Marcot, B.G., and Ellis, R. 2006. Bayesian belief networks: applications in ecology and natural resource management. Can. J. For. Res. **36**(12): 3053–3062. doi:10.1139/x06-238.

McKinney, M.L., and Lockwood, J.L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol. Evol. **14**(11): 450–453. doi:10.1016/S0169-5347(99)01679-1.

McMahon, T.E., and Bennett, D.H. 1996. Walleye and northern pike: boost or bane to northwest fisheries? Fisheries **21**(8): 6–13. doi:10.1577/1548-8446(1996)021.

Mingelbier, M., Brodeur, P., and Morin, J. 2008. Spatially explicit model predicting the spawning habitat and early stage mortality of northern pike (*Esox lucius*) in a large system: the St. Lawrence River between 1960 and 2000. Hydrobiologia **601**(1): 55–69. doi:10.1007/s10750-007-9266-z.

Mooney, H.A., and Cleland, E.E. 2001. The evolutionary impact of invasive species. Proc. Natl. Acad. Sci. **98**(10): 5446–5451. doi:10.1073/pnas.091093398.

Morrow, J.E. 1980. The freshwater fishes of Alaska. Alaska Northwest Publishing Company, Anchorage.

Moyle, P.B., and Leidy, R.A. 1992. Loss of biodiversity in aquatic ecosystems: evidence from fish faunas. *In* Conservation Biology The Theory and Practice of Nature Conservation and Management, 1st edition. *Edited by* P.L. Fiedler and S.K. Jain. Chapman and Hall, New York and London. pp. 127–169.

Moyle, P.B., and Light, T. 1996a. Fish invasions in California: do abiotic factors determine success? Ecology **77**(6): 1666–1670. doi:10.2307/2265770.

Moyle, P.B., and Light, T. 1996b. Biological invasions of fresh water: Empirical rules and assembly theory. Biol. Conserv. **78**(1–2): 149–161. doi:10.1016/0006-3207(96)00024-9.

Nicholson, M.E., Rennie, M.D., and Mills, K.H. 2015. Apparent extirpation of prey fish communities following the introduction of northern pike (*Esox lucius*). Can. Field-Naturalist **129**(2): 165. doi:10.22621/cfn.v129i2.1697.

Olden, J.D., Vander Zanden, M.J., and Johnson, P.T.J. 2011. Assessing ecosystem vulnerability to invasive rusty crayfish (*Orconectes rusticus*). Ecol. Appl. **21**(7): 2587–2599. doi:10.1890/10-2051.1.

Patankar, R., von Hippel, F.A., and Bell, M.A. 2006. Extinction of a weakly armoured threespine stickleback (*Gasterosteus aculeatus*) population in Prator Lake, Alaska. Ecol. Freshw. Fish **15**(4): 482–487. doi:10.1111/j.1600-0633.2006.00186.x.

Pauly, D. 1989. A simple index of metabolic level in fishes. Fishbyte, Newsl. Netw. Trop. Fish. Sci. **7**(1): 22.

Peake, S.J. 2008. Swimming performance and behaviour of fish species endemic to Newfoundland and Labrador: A literature review for the purpose of establishing design and water velocity criteria for fishways and culverts. Can. Manuscr. Rep. Fish. Aquat. Sci. **2843**: v+52.

Petersen, J.H., and Deangelis, D.L. 2000. Dynamics of prey moving through a predator field: A model of migrating juvenile salmon. Math. Biosci. **165**(2): 97–114. doi:10.1016/S0025-5564(00)00017-1.

Peterson, D.P., Rieman, B.E., Dunham, J.B., Fausch, K.D., and Young, M.K. 2008. Analysis of trade-offs between threats of invasion by nonnative brook trout (*Salvelinus fontinalis*) and intentional isolation for native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). Can. J. Fish. Aquat. Sci. **65**(4): 557–573. doi:10.1139/f07-184.

Peterson, D.P., Wenger, S.J., Rieman, B.E., and Isaak, D.J. 2013. Linking climate change and fish conservation efforts using spatially explicit decision support tools. Fisheries **38**(3): 112–127. doi:10.1080/03632415.2013.769157.

Peterson, E.E., and Ver Hoef, J.M. 2014. STARS: An ArcGIS toolset used to calculate the spatial information needed to fit spatial statistical models to stream network data. J. Stat. Softw. **56**(2): 1–17. doi:http://dx.doi.org/10.18637/jss.v056.i02.

Quinn, T.P. 2005. Downstream migration: to sea or not to sea? *In* The behavior and ecology of Pacific salmon and trout, 1st edition. University of Washington Press, Vancouver. pp. 209–228.

Raat, A.J.P. 1988. Synopsis of biological data on the northern pike *Esox lucius* Linnaeus, 1758. Rome.

Radinger, J., and Wolter, C. 2014. Patterns and predictors of fish dispersal in rivers. Fish Fish. **15**(3): 456–473. doi:10.1111/faf.12028.

Rahel, F.J. 2002. Homogenization of freshwater faunas. Annu. Rev. Ecol. Syst. **33**(1): 291–315. doi:10.1146/annurev.ecolsys.33.010802.150429.

Rahel, F.J. 2007. Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. Freshw. Biol. **52**(4): 696–710. doi:10.1111/j.1365-2427.2006.01708.x.

Ribeiro, F., and Leunda, P.M. 2012. Non-native fish impacts on Mediterranean freshwater ecosystems: Current knowledge and research needs. Fish. Manag. Ecol. **19**(2): 142–156. doi:10.1111/j.1365-2400.2011.00842.x.

Rincon, P.A., Velasco, J.C., Gonzalez-Sanchez, N., and Pollo, C. 1990. Fish assemblages in small streams in western Spain: The influence of an introduced predator. doi:http://dx.doi.org/10.1002/aqc.679.

Romey, B.T. 2018. Modeling spawning habitat potential for chum (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) in relation to landscape characteristics in coastal Southeast Alaska. Portland State University 2018.

Rose, P.M., Kennard, M.J., Moffatt, D.B., Sheldon, F., and Butler, G.L. 2016. Testing three species distribution modelling strategies to define fish assemblage reference conditions for stream bioassessment and related applications. PLoS One **11**(1): 1–23. doi:10.1371/journal.pone.0146728.

Rutz, D.S. 1996. Seasonal movements, age and size statistics, and food habits of upper Cook Inlet Northern Pike during 1994 and 1995. Anchorage.

Rutz, D.S. 1999. Movements, food availability and stomach contents of northern pike in selected Susitna River Drainages, 1996-1997. Anchorage.

Schmitt, C.J., Lemly, A.D., and Winger, P. V. 1993. Habitat suitability index model for brook trout. Washington, D.C.

Schwoerer, T. 2017. Invasive elodea threatens remote ecosystem services in Alaska: A spatially-explicit bioeconomic risk analysis. University of Alaska Fairbanks. doi:10.13140/RG.2.2.22859.59682.

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. *In* Fisheries Research Board of Canada Bulletin, 1st edition. Ottawa.

Sepulveda, A., Ray, A., Al-chokhachy, R., Muhlfeld, C., Gressw, R., Gross, J., and Kershner, J. 2012. Aquatic invasive species: lessons from cancer research for preventing the spread of harmful invasive species. Am. Sci. **100**. doi:10.1511/2012.96.234.

Sepulveda, A.J., Rutz, D.S., Dupuis, A.W., Shields, P.A., and Dunker, K.J. 2015. Introduced northern pike consumption of salmonids in southcentral Alaska. Ecol. Freshw. Fish **24**(4): 519–531. doi:10.1111/eff.12164.

Sepulveda, A.J., Rutz, D.S., Ivey, S.S., Dunker, K.J., and Gross, J.A. 2013. Introduced northern pike predation on salmonids in southcentral Alaska. Ecol. Freshw. Fish **22**(2): 268–279. doi:10.1111/eff.12024.

Shallin Busch, D., Sheer, M., Burnett, K., McElhany, P., and Cooney, T. 2013. Landscape-level model to predict spawning habitat for lower Columbia River fall Chinook salmon (*Oncorhynchus tshawytscha*). River Res. Appl. **29**(3): 297–312. doi:10.1002/rra.1597.

Sih, A., Bolnick, D.I., Luttbeg, B., Orrock, J.L., Peacor, S.D., Pintor, L.M., Preisser, E., Rehage, J.S., and Vonesh, J.R. 2010. Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos **119**(4): 610–621. doi:10.1111/j.1600-0706.2009.18039.x.

Skov, C., Lucas, M.C., and Jacobsen, L. 2018. Spatial ecology. *In* Biology and Ecology of Pike, 1st edition. *Edited by* C. Skov and P.A. Nilsson. CRC Press, Boca Raton. pp. 83–120. Available from https://www.crcpress.com/Biology-and-Ecology-of-Pike/Skov-Nilsson/p/book/9781482262902.

Smukall, M. 2015. Northern pike investigations final report (2012 – 2014). Soldotna, Alaska.

Spens, J., Englund, Gör., and Lundqvist, H. 2007. Network connectivity and dispersal barriers: using geographical information system (GIS) tools to predict landscape scale distribution of a key predator (Esox lucius) among lakes. J. Appl. Ecol. **44**(6): 1127–1137. doi:10.1111/j.1365-2664.2007.01382.x.

United States Geological Survey. 2004. National Hydrography Dataset. Available from https://nhd.usgs.gov/NHD_High_Resolution.html [accessed 1 January 2018].

United States Geological Survey. 2013. National Hydrography Geodatabase: The National Map viewer. Available from https://viewer.nationalmap.gov/viewer/nhd.html?p=nhd.

Uusitalo, L. 2007. Advantages and challenges of Bayesian Networks in environmental modelling. Ecol. Modell. **203**(3–4): 312–318. doi:10.1016/j.ecolmodel.2006.11.033.

van Kleef, H., van der Velde, G., Leuven, R.S.E.W., and Esselink, H. 2008. Pumpkinseed sunfish (*Lepomis gibbosus*) invasions facilitated by introductions and nature management strongly reduce macroinvertebrate abundance in isolated water bodies. Biol. Invasions **10**(8): 1481–1490. doi:10.1007/s10530-008-9220-7.

Vitousek, P.M., DAntonio, C.M., Loope, L.L., and Westbrooks, R. 1996. Biological invasions as global environmental change. Am. Sci. **84**(5): 468–478. doi:1996AmSci..84..468V.

Woll, C. 2015. Landscape-scale mapping of Pacific salmon and their freshwater habitats in the Mat-Su Basin. The Nature Conservancy. Available from http://www.conservationgateway.org/ConservationByGeography/NorthAmerica/UnitedStates/alaska/scak/science/mapping/Documents/Landscape_scale_mapping_of_Pacific_Salmon_and_their_freshwater_habitats_in_the_Mat_Su_Basin.pdf.

Vander Zanden, M.J., and Olden, J.D. 2008. A management framework for preventing the secondary spread of aquatic invasive species. Can. J. Fish. Aquat. Sci. **65**(7): 1512–1522. doi:10.1139/F08-099.

Vander Zanden, M.J., Olden, J.D., Thorne, J.H., and Mandrak, N.E. 2004. Predicting occurrences and impacts of smallmouth bass introductions in north-temperate lakes. Ecol. Appl. **14**(1): 132–148. doi:10.1890/02-5036.

Figures

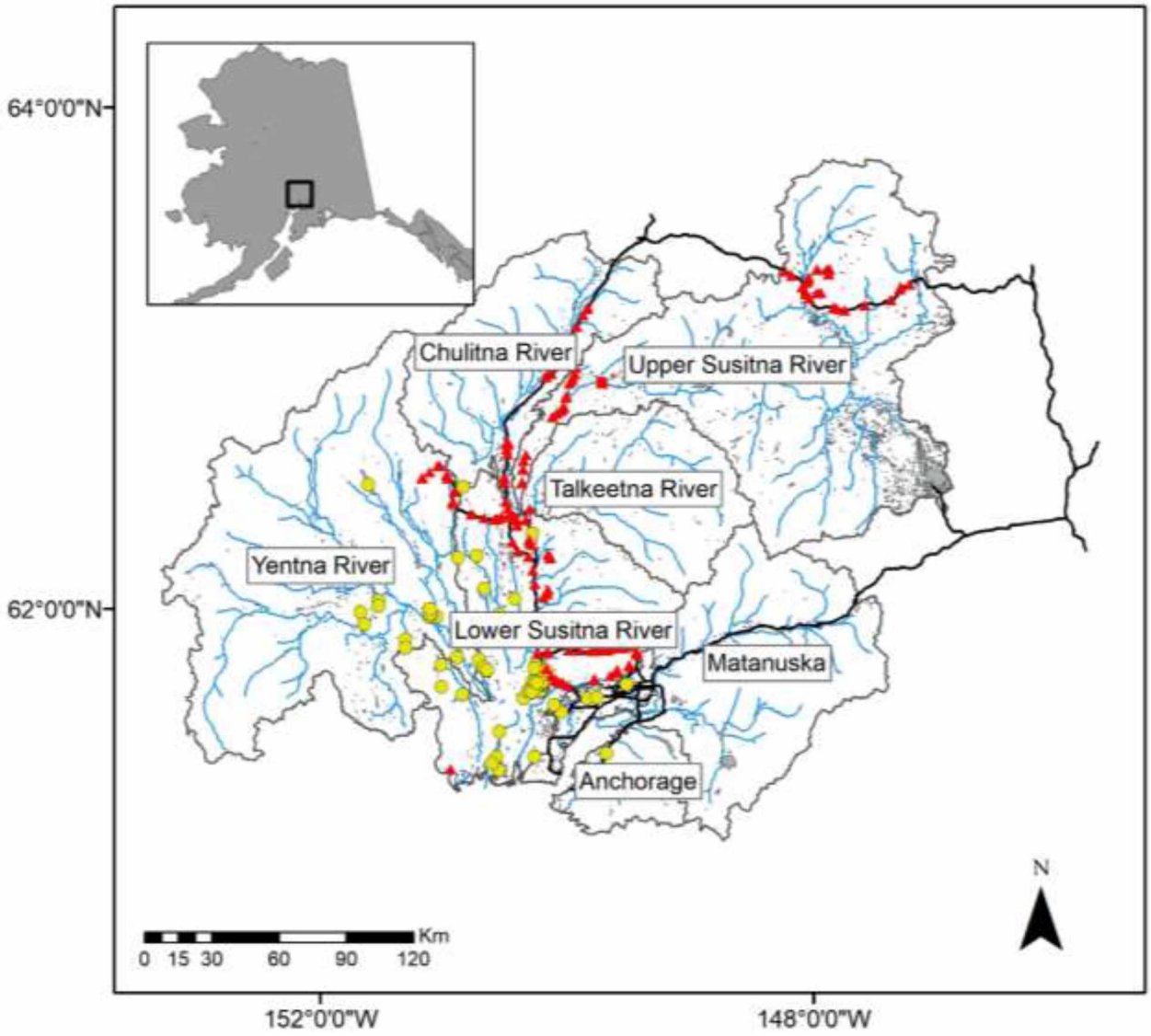


Figure 2.1. Map of Matanuska-Susitna basin, Southcentral Alaska, USA showing stream reaches (blue lines), sub-basin delineations (grey lines), barriers to fish passage (culverts: red triangle; Devil's Canyon: red square), major roads (black lines), significant lakes (grey polygons), and known invaded lakes (yellow circles).

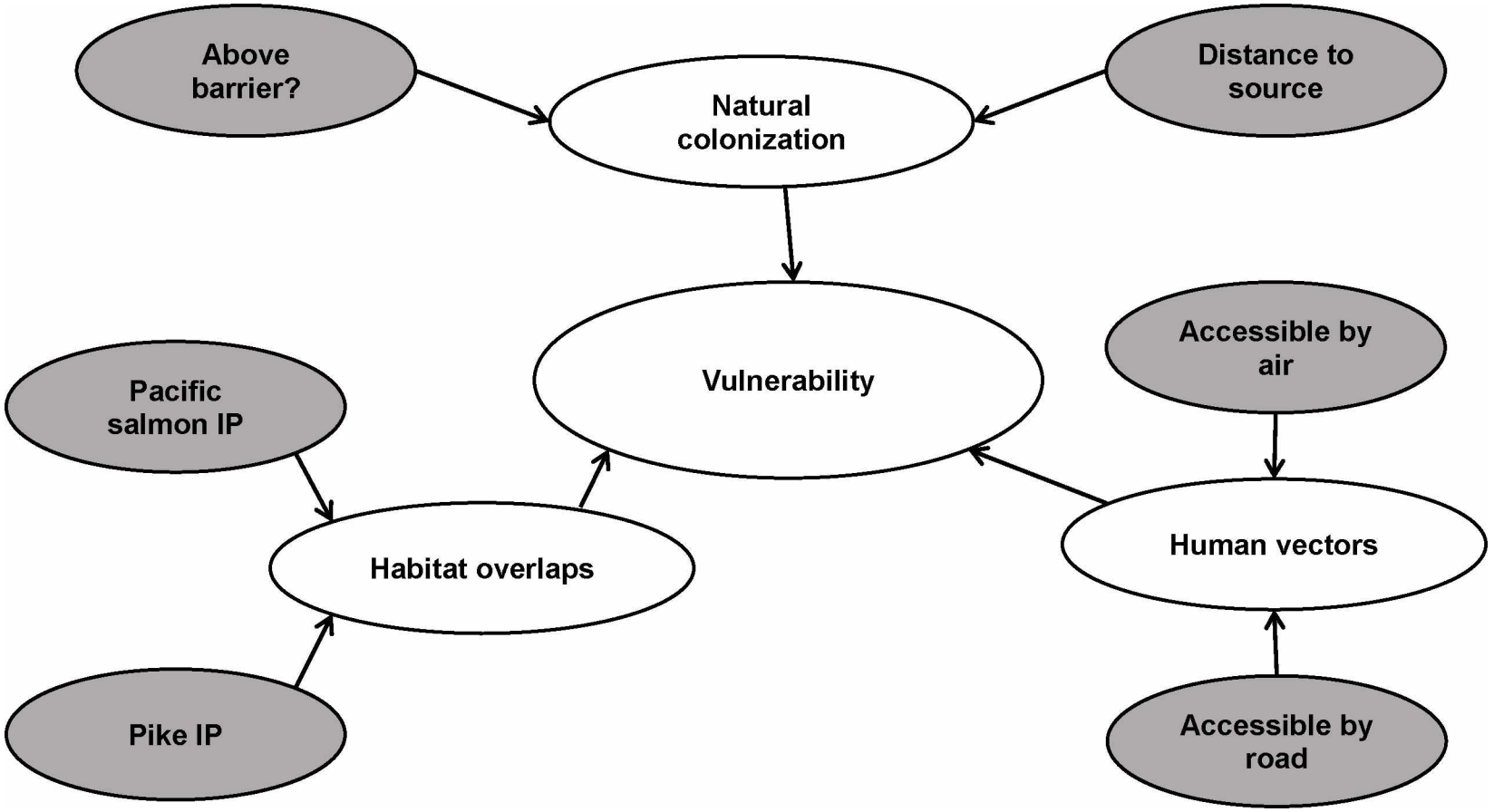


Figure 2.2. Conceptual diagram depicting factors hypothesized to affect Pacific salmon vulnerability to invasion by northern pike in the Matanuska-Susitna basin (Southcentral Alaska, USA). Shaded ovals represent input variables in the Bayesian network (Table 1). See Table 1 for definitions of nodes and states within nodes.

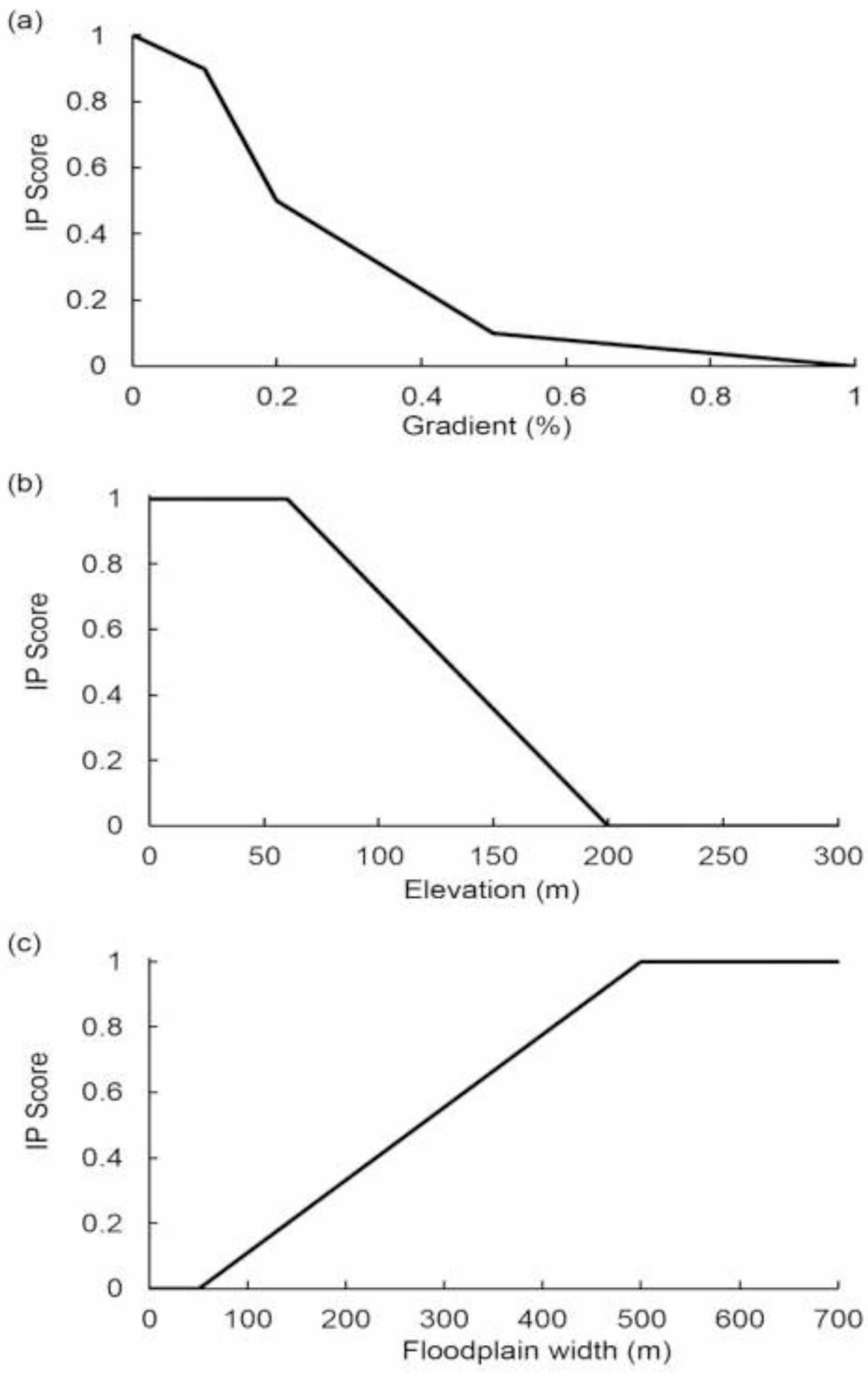


Figure 2.3. Intrinsic potential (IP) curves for northern pike for three attributes: (a) gradient (%); (b) elevation (m); and (c) floodplain width (m).

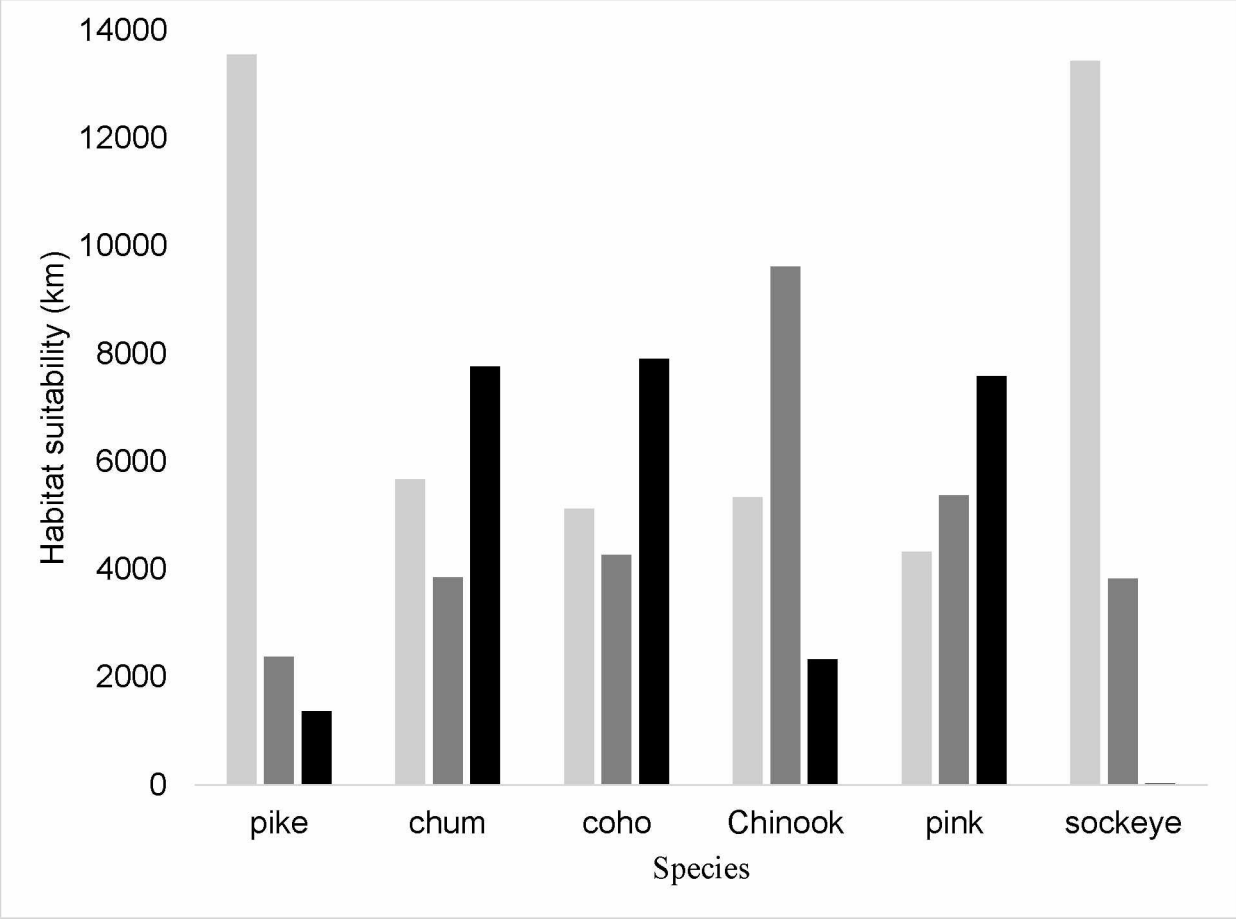


Figure 2.4. Habitat potential (km) for northern pike and Pacific salmon in the Matanuska-Susitna basin, Alaska, USA. Light grey represents low-potential, dark grey represents moderate-potential, and black represents high-potential habitat.

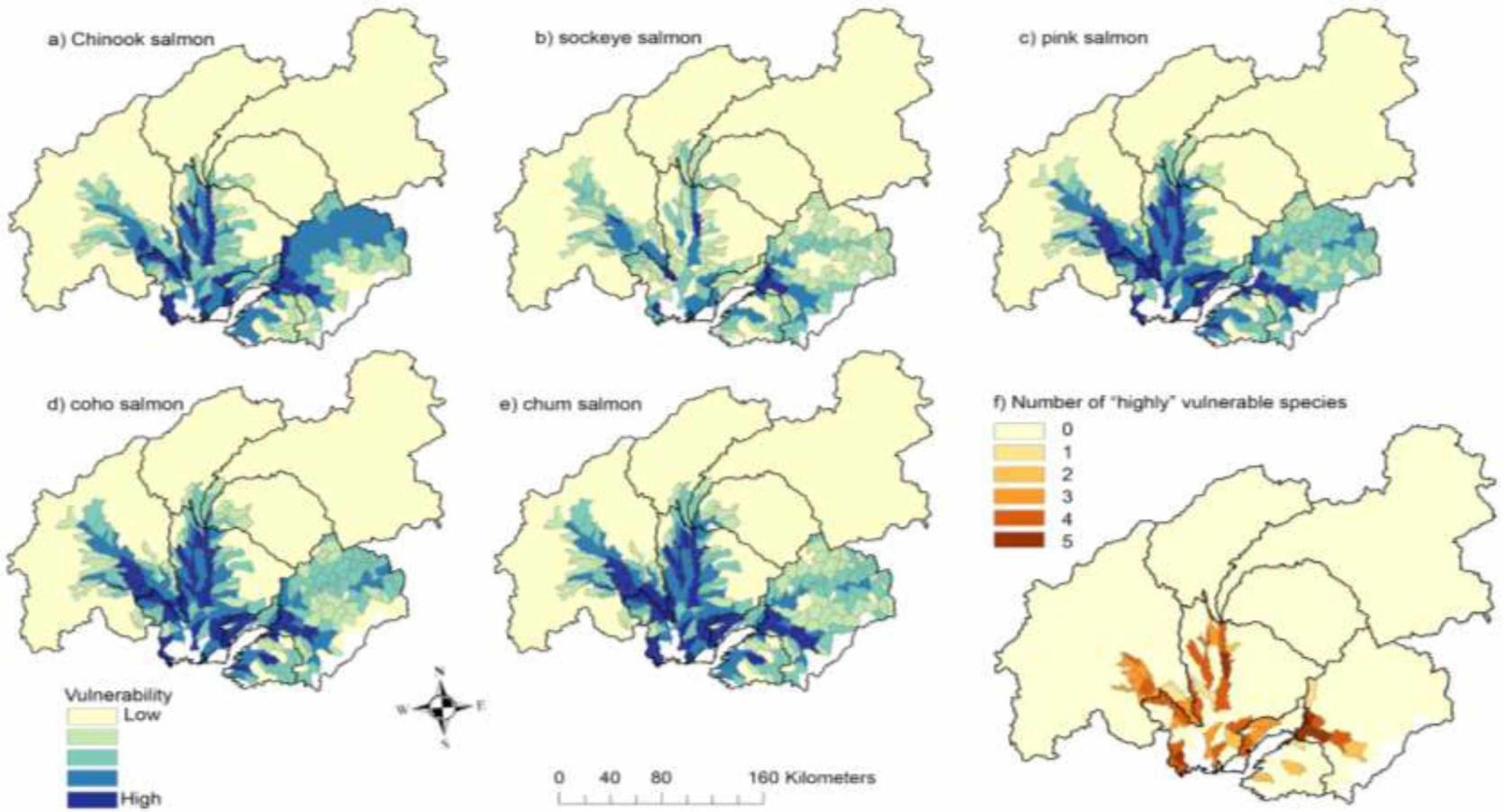


Figure 2.5. Vulnerability of Pacific salmon to invasion by northern pike for the Matanuska-Susitna basin (Southcentral, Alaska, USA). Species-specific estimates shown in panels a – e and a composite "highly-vulnerable" estimate shown in panel f. Black lines represent sub-basins. Darker colors represent higher vulnerability with species-specific vulnerability shown in blues and the number of species identified as "high" vulnerability shown in oranges.

Tables

Table 2.1. Node definitions and states for a Bayesian belief network to assess vulnerability of juvenile salmon to introduced northern pike in the Matanuska-Susitna River basin, Southcentral Alaska, USA.

Node Name	Definition	State
Natural colonization	The potential for northern pike to colonize by natural means	none low moderate high
Distance to invaded waterbody (I)	In-stream distance to nearest invaded lake	close: < 1 000 m moderate: 1 000 – 10 000 m far: > 10 000 m
Above barrier? (I)	Whether the stream reach is located above a known barrier	yes: 1 no: 0
Human-mediated colonization	The potential for northern pike to be introduced by humans	low moderate high
Accessible by road (I)	The potential for introduction by roadway	close: < 1 200 m moderate: 1 200 – 3 600 m far: > 3 600 m

Accessible by plane (I)	The potential for introduction by five types of single-engine aircraft, common to the Matanuska-Susitna basin as measured by the sum of lake ranks within a HUC-12 unit	none: 0 low: 0 – 10 moderate: 11 – 20 high: > 20
Habitat overlap	The potential for overlap of different quality habitat between northern pike and salmon	low moderate high
Intrinsic potential northern pike	The habitat potential for northern pike as measured for a given reach using gradient, elevation, and floodplain	low: < 0.25 moderate: 0.25 – 0.75 high: > 0.75
Intrinsic potential Chinook salmon (I)	The habitat potential for Chinook salmon as measured for a given reach	low: < 0.25 moderate: 0.25 – 0.75 high: > 0.75
Intrinsic potential chum salmon (I)	The habitat potential for chum salmon as measured for a given reach	low: < 0.25 moderate: 0.25 – 0.75 high: > 0.75

Intrinsic potential coho salmon (I)	The habitat potential for coho salmon as measured for a given reach	low: 0 – 1 moderate: 2 – 3 high: 4
Intrinsic potential pink salmon (I)	The habitat potential for pink salmon as measured for a given reach	low: < 0.25 moderate: 0.25 – 0.75 high: > 0.75
Intrinsic potential sockeye salmon (I)	The habitat potential for sockeye salmon as measured for a given reach	low: 0 – 1 moderate: 2 – 3 high: 4
Vulnerability to invasion	The vulnerability to invasion by northern pike, for each Pacific salmon	low moderate high

Note: Input nodes (I) are assigned the probability of being in each state

Table 2.2. Total length (km) of highly vulnerable stream reaches for five Pacific salmon species to northern pike within the Matanuska-Susitna basin, Alaska, USA by HUC-8 sub-basin. Total area (km^2) and length of streams (km) in each sub-basin are also shown. Values in parenthesis represent the species-specific proportion of highly vulnerable habitat.

Sub-basin	Area	Stream length					
(HUC-8)	(km2)	(km)	chum	coho	Chinook	pink	sockeye
Anchorage	3061	939	233	250	129	229	116
			(0.09)	(0.1)	(0.08)	(0.09)	(0.1)
Matanuska	8662	2393	258	240	147	272	145
			(0.1)	(0.09)	(0.09)	(0.11)	(0.12)
Upper Susitna River	16346	5546	13	14	4 (0)	4 (0)	4 (0)
			(0.01)	(0.01)			
Chulitna River	6728	2280	27	28	11	19	11
			(0.01)	(0.01)	(0.01)	(0.01)	(0.01)
Talkeetna River	5286	1681	41	32	13	29	13
			(0.02)	(0.01)	(0.01)	(0.01)	(0.01)
Yentna River	15869	5988	557	516	280	548	325
			(0.22)	(0.2)	(0.17)	(0.22)	(0.27)
Lower Susitna River	8855	4049	1428	1456	1078	1356	581
			(0.56)	(0.57)	(0.65)	(0.55)	(0.49)

Appendices

Appendix 2.A. Creation of the landscape network

The following steps were modified from the STARS user manual (available from: https://www.fs.fed.us/rm/boise/AWAE/projects/SSN_STARS/software_data.html#STARS) and performed by a custom ArcMap toolbox to create a landscape network (LSN) prior to creation of the spatial stream network (SSN). The R package *SSN* version 1.1.12 was used to calculate the pair-wise distance between reaches ('sites') and closest known source lakes ('preds').

1) The seven NetMap sub-basins were *Merged* and the resulting network pruned to reaches with an upstream area greater than 5 km^2.
2) The stream network was *Dissolved* into a single polyline,
3) The endpoints of each reach identified using *Feature Vertices to Points* > *both_ends*
4) The network *split* at each point using the editor in ArcMap.
5) Stream flow direction was corrected to ensure downstream flow throughout the stream network using *Reverse Flow Direction*.
6) The resulting polyline was turned into a topologically corrected LSN by running the following in STARS:
    a. *Identify complex confluences*
    b. *Check network topology*
7) The centroid of all stream reaches, and invaded lakes were identified using *Feature to Point* and added to the SSN as 'sites' and 'predictions' (see STARS for details).
8) Five STARS tools were used to generate the spatial data necessary for conversion to the SSN.
    a. *Segment PI*

b. *Additive Function – Edges*

c. *Additive Function – Sites*

d. *Upstream Distance – Edges*

e. *Upstream Distance – Sites*

Conditional probability tables for Pacific salmon vulnerability belief network

Appendix 2.B. Conditional probability table for habitat overlap of Pacific salmon with northern pike in the Matanuska-Susitna basin, Alaska, USA.

Input node		State (Habitat overlap)		
IP_PIKE	IP_SALMON	low	moderate	high
low	low	100	0	0
low	moderate	60	40	0
low	high	50	30	20
moderate	low	60	40	0
moderate	moderate	0	100	0
moderate	high	0	30	70
high	low	0	25	75
high	moderate	0	15	85
high	high	0	0	100

Appendix 2.C. Conditional probability table for natural colonization of northern pike in the Matanuska-Susitna basin, Alaska, USA.

Input node		State (Natural colonization)			
BARR	DISTPIKE	none	low	moderate	high
yes	close	10	50	35	5
yes	moderate	10	70	15	5
yes	far	15	80	5	0
no	close	0	0	0	100
no	moderate	0	0	100	0
no	far	0	100	0	0

Appendix 2.D. Conditional probability table for human-mediated colonization of northern pike in the Matanuska-Susitna basin, Alaska, USA.

Input node		State (Human-mediated colonization)		
AIR	ROAD	low	moderate	high
none	close	10	10	80
none	moderate	25	25	50
none	far	80	10	10
low	close	0	15	85
low	moderate	20	30	50
low	far	50	30	20
moderate	close	0	10	90
moderate	moderate	10	30	60
moderate	far	0	40	60
high	close	0	0	100
high	moderate	0	10	90
high	far	0	20	80

Appendix 2.E. Conditional probability table for vulnerability of Pacific salmon in the Matanuska-Susitna basin, Alaska, USA.

Input nodes			State (Vulnerability)		
habitat	natural	human	low	moderate	high
low	none	low	90	5	5
low	none	moderate	85	10	5
low	none	high	80	15	5
low	low	low	85	10	5
low	low	moderate	80	15	5
low	low	high	75	20	5
low	moderate	low	70	25	5
low	moderate	moderate	65	30	5
low	moderate	high	60	35	5
low	high	low	55	40	5
low	high	moderate	50	45	5
low	high	high	45	50	5
moderate	none	low	55	40	5
moderate	none	moderate	50	45	5
moderate	none	high	45	50	5
moderate	low	low	50	45	5
moderate	low	moderate	45	50	5
moderate	low	high	40	55	5

moderate	moderate	low	30	60	10
moderate	moderate	moderate	25	50	25
moderate	moderate	high	20	55	25
moderate	high	low	10	60	30
moderate	high	moderate	5	45	50
moderate	high	high	5	40	55
high	none	low	10	60	30
high	none	moderate	5	45	50
high	none	high	5	40	55
high	low	low	5	45	50
high	low	moderate	5	40	55
high	low	high	5	35	60
high	moderate	low	5	25	70
high	moderate	moderate	5	20	75
high	moderate	high	0	20	80
high	high	low	0	10	90
high	high	moderate	0	5	95
high	high	high	0	0	100

Appendix 2.F. Description of parameters used to estimate lake accessibility by float planes. Lakes were ranked by minimum fetch (plane data from Schwoerer 2017).

Rank	Type of single engine plane	Range (km)	Minimum fetch of destination (m)
1	Piper PA-17, PA-18, Tailorcraft	493	336
2	Other and not specified	1030	498
3	DeHavilland DHC-2 Beaver	732	505
4	Cessna-172 to 206	1325	511
5	DeHavilland DHC-3 Otter	1520	645

Appendix 2.G. Weighting for conditional probability table for vulnerability of Pacific salmon in the Matanuska-Susitna basin, Alaska, USA (Appendix E). Ranks were weighted as follows: habitat overlap (Input node = habitat; high = 100), natural colonization (Input node = natural; high = 50), and human-mediated colonization (Input node = human; high = 10). The total possible weighted rank was 160, thus we used 80 as the inflection point for shifting vulnerability from low towards high.

Input nodes			Weighted ranks				State (Vulnerability)		
habitat	natural	human	habitat	natural	human	sum	low	moderate	high
low	none	low	0	0	0	0	90	5	5
low	none	moderate	0	0	5	5	85	10	5
low	low	low	0	5	0	5	85	10	5
low	none	high	0	0	10	10	80	15	5
low	low	moderate	0	5	5	10	80	15	5
low	low	high	0	5	10	15	75	20	5
low	moderate	low	0	25	0	25	70	25	5
low	moderate	moderate	0	25	5	30	65	30	5
low	moderate	high	0	25	10	35	60	35	5
low	high	low	0	50	0	50	55	40	5
moderate	none	low	50	0	0	50	55	40	5

low	high	moderate	0	50	5	55	50	45	5
moderate	none	moderate	50	0	5	55	50	45	5
moderate	low	low	50	5	0	55	50	45	5
low	high	high	0	50	10	60	45	50	5
moderate	none	high	50	0	10	60	45	50	5
moderate	low	moderate	50	5	5	60	45	50	5
moderate	low	high	50	5	10	65	40	55	5
moderate	moderate	low	50	25	0	75	30	60	10
moderate	moderate	moderate	50	25	5	80	25	50	25
moderate	moderate	high	50	25	10	85	20	55	25
moderate	high	low	50	50	0	100	10	60	30
high	none	low	100	0	0	100	10	60	30
moderate	high	moderate	50	50	5	105	5	45	50
high	none	moderate	100	0	5	105	5	45	50
high	low	low	100	5	0	105	5	45	50
moderate	high	high	50	50	10	110	5	40	55
high	none	high	100	0	10	110	5	40	55
high	low	moderate	100	5	5	110	5	40	55

high	low	high	100	5	10	115	5	35	60
high	moderate	low	100	25	0	125	5	25	70
high	moderate	moderate	100	25	5	130	5	20	75
high	moderate	high	100	25	10	135	0	20	80
high	high	low	100	50	0	150	0	10	90
high	high	moderate	100	50	5	155	0	5	95
high	high	high	100	50	10	160	0	0	100

Species specific vulnerability

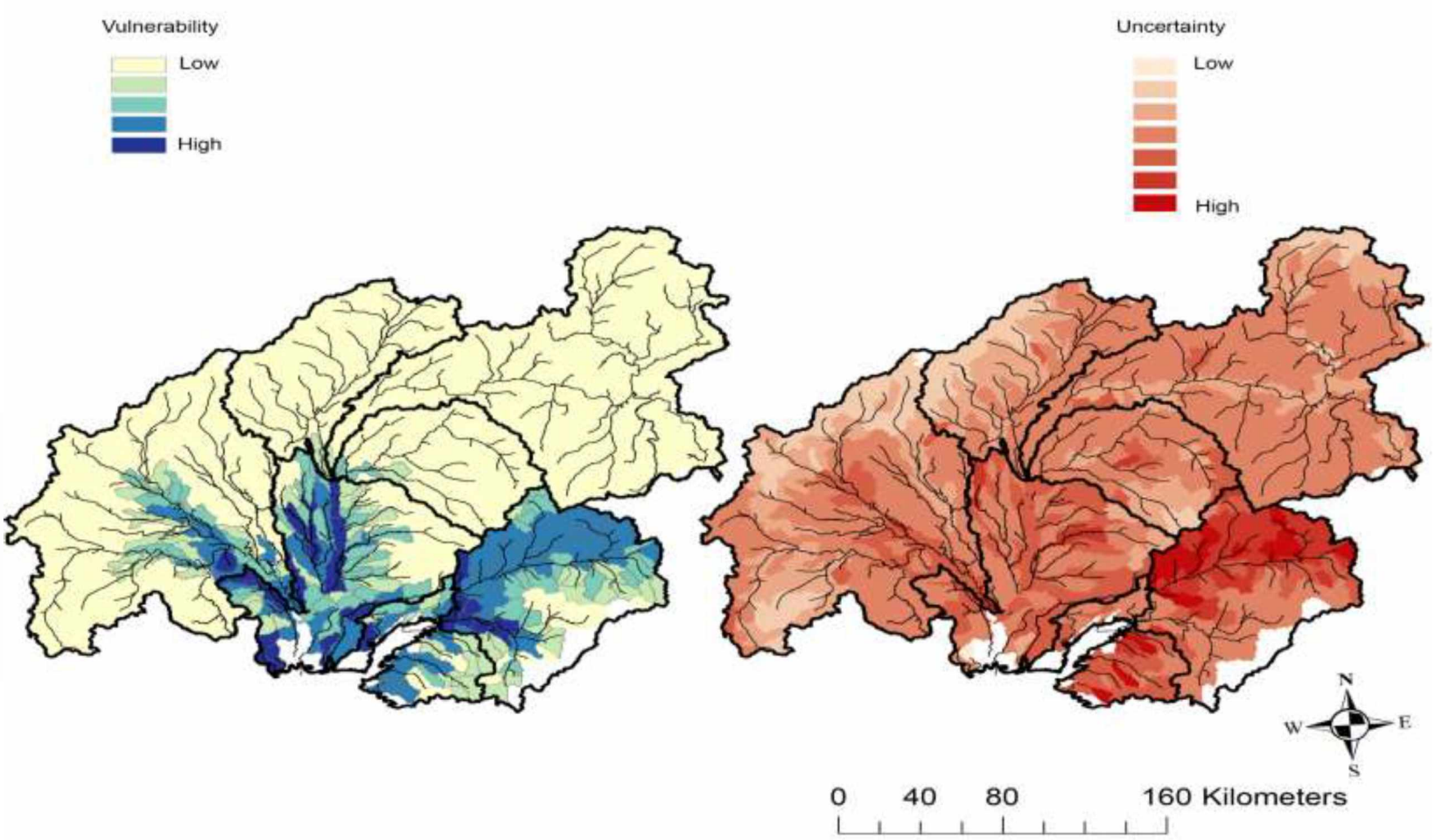
Appendix 2.H. Vulnerability of Pacific salmon by HUC-8 sub-basin in stream kilometers within the Matanuska-Susitna basin, Alaska, USA. Table represents Netica vulnerability class 'moderate'.

Sub-basin	Area	Stream length					
(HUC-8)	(km^2)	(km)	chum	coho	Chinook	pink	sockeye
Anchorage	3061	939	177	201	336	212	157
Matanuska	8662	2393	989	1142	1502	1189	788
Upper Susitna River	16346	5546	51	52	9	50	38
Chulitna River	6728	2280	67	66	30	75	53
Talkeetna River	5286	1681	53	48	53	63	44
Yentna River	15869	5988	443	485	485	400	262
Lower Susitna River	8855	4049	635	626	819	692	362

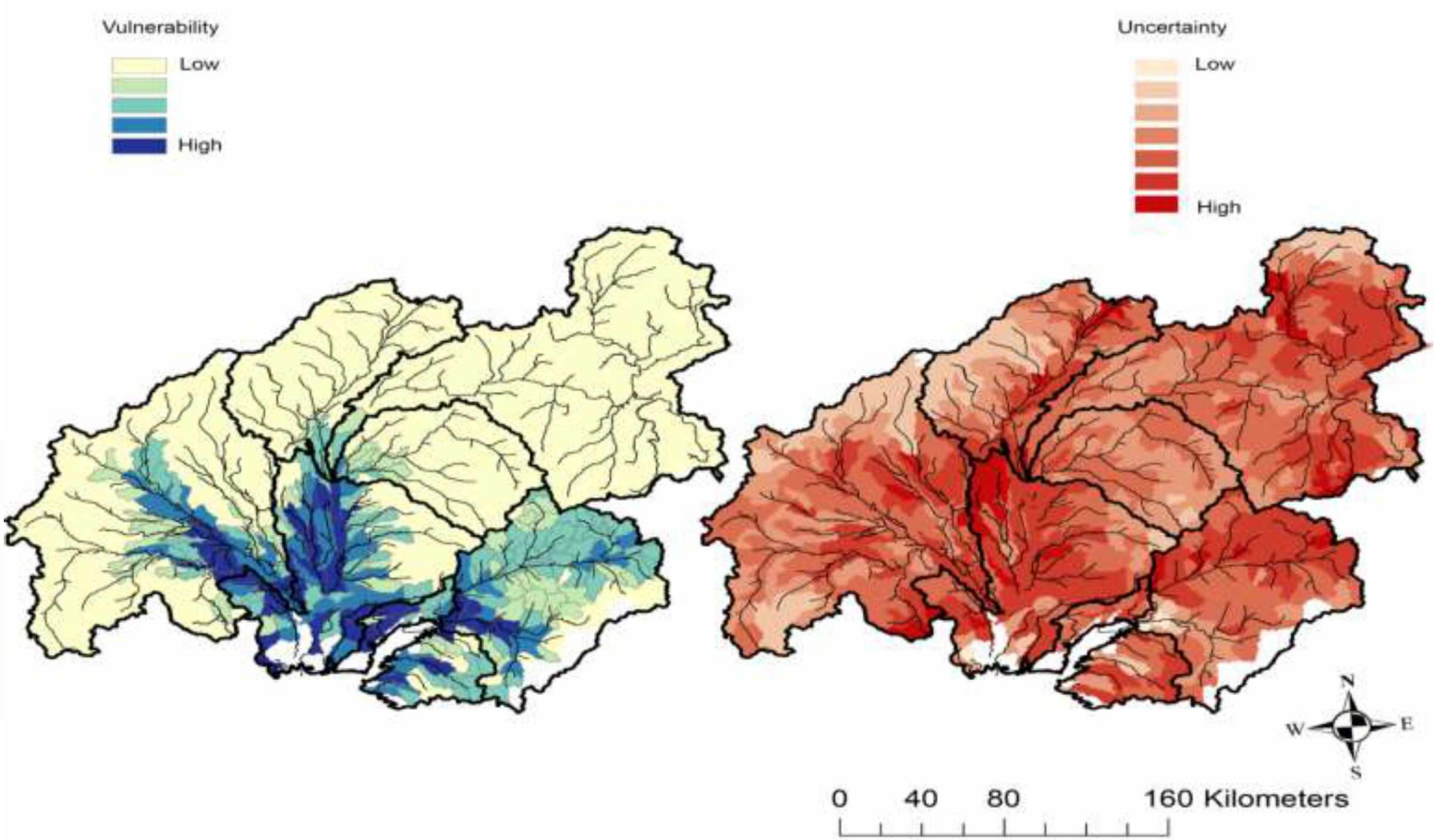
Appendix 2.I. Vulnerability of Pacific salmon by HUC-8 sub-basin in stream kilometers within the Matanuska-Susitna basin, Alaska, USA. Table represents Netica vulnerability class 'low'.

Sub-basin	Area	Stream length					
(HUC-8)	(km^2)	(km)	chum	coho	Chinook	pink	sockeye
Anchorage	3061	939	291	250	236	261	428
Matanuska	8662	2393	1126	992	724	912	1440
Upper Susitna River	16346	5546	412	410	462	422	433
Chulitna River	6728	2280	2151	2151	2204	2150	2181
Talkeetna River	5286	1681	1587	1602	1615	1588	1624
Yentna River	15869	5988	4968	4967	5202	5020	5381
Lower Susitna River	8855	4049	1783	1763	1948	1797	2902

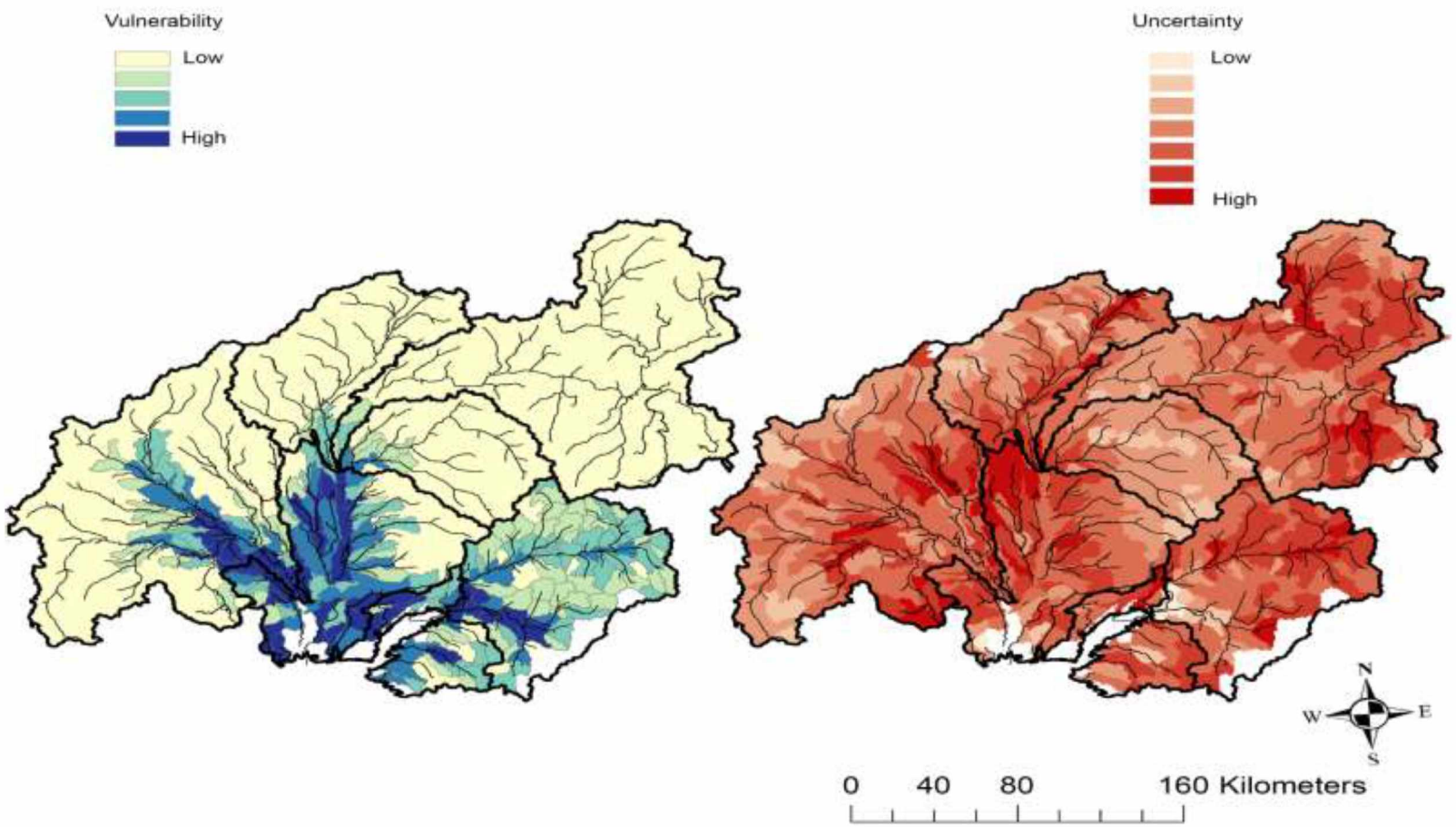
Appendix 2.J. Dam that was constructed by unknown individuals at the outlet of Bulchitna Lake (Susitna, Alaska, USA) to contain pike, but overtopped by high water events. Photo taken by the author in August of 2017.



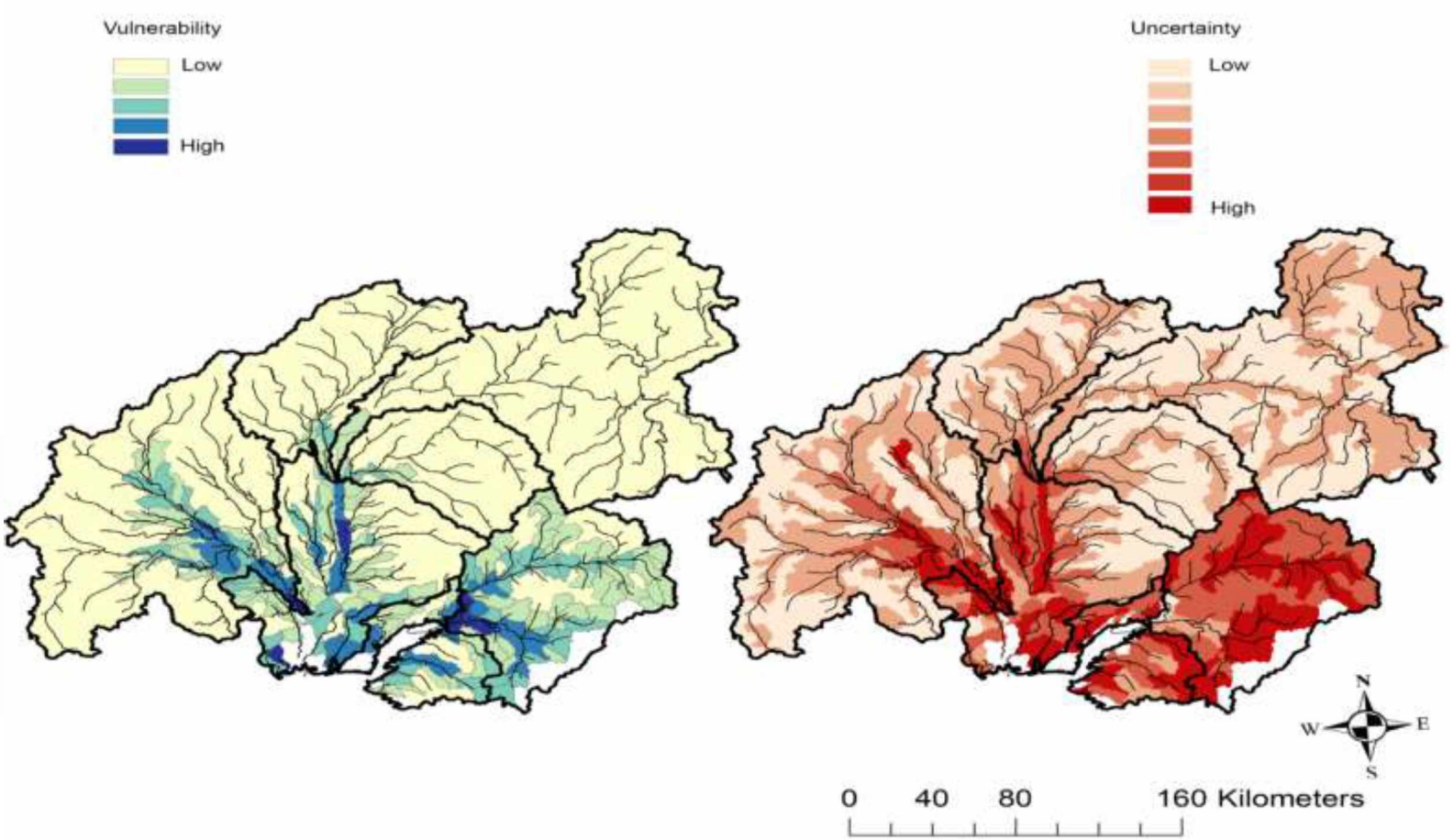
Appendix 2.K. Vulnerability estimates and associated uncertainty of Chinook salmon to invasion of northern pike in the Matanuska-Susitna basin (Southcentral, Alaska, USA). Darker colors represent higher values. See text for details on how vulnerability was assessed.



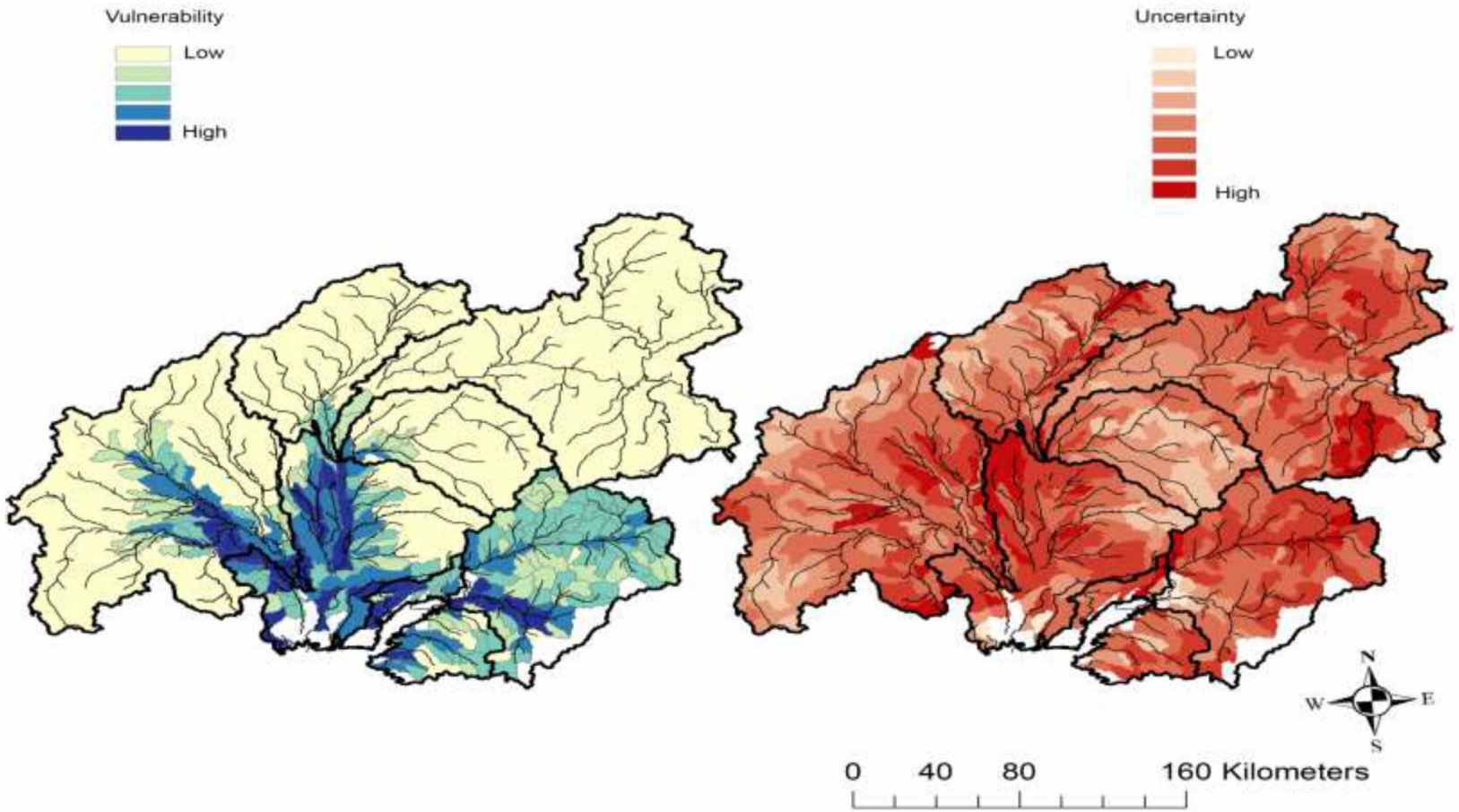
Appendix 2.L. Vulnerability estimates and associated uncertainty of coho salmon to invasion of northern pike in the Matanuska-Susitna basin (Southcentral, Alaska, USA). Darker colors represent higher values. See text for details on how vulnerability was assessed.



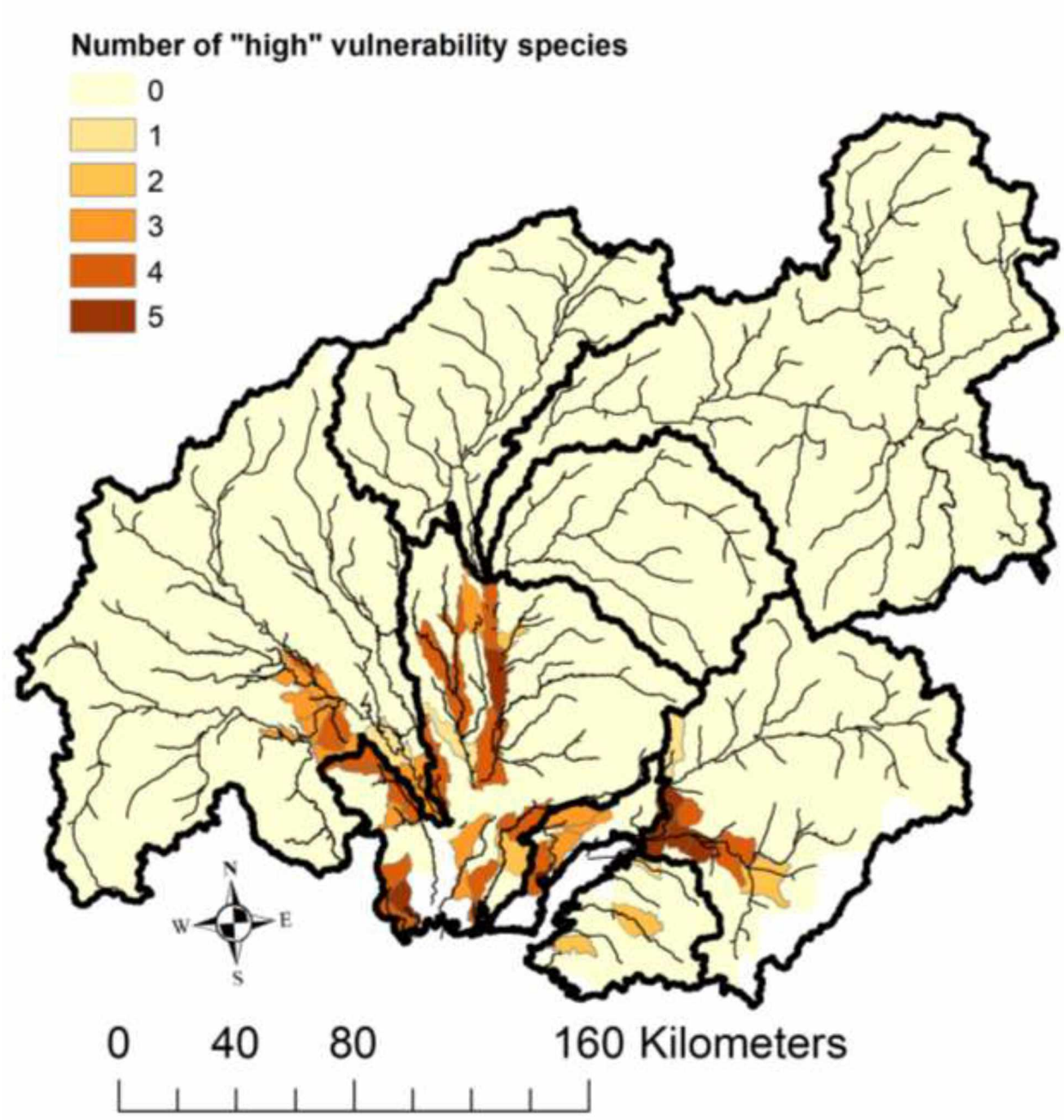
Appendix 2.M. Vulnerability estimates and associated uncertainty of chum salmon to invasion of northern pike in the Matanuska-Susitna basin (Southcentral, Alaska, USA). Darker colors represent higher values. See text for details on how vulnerability was assessed.



Appendix 2.N. Vulnerability estimates and associated uncertainty of sockeye salmon to invasion of northern pike in the Matanuska-Susitna basin (Southcentral, Alaska, USA). Darker colors represent higher values. See text for details on how vulnerability was assessed.



Appendix 2.O. Vulnerability estimates and associated uncertainty of pink salmon to invasion of northern pike in the Matanuska-Susitna basin (Southcentral, Alaska, USA). Darker colors represent higher values. See text for details on how vulnerability was assessed.



Appendix 2.P. The number of "highly" vulnerable Pacific salmon species, by sub-basin, to invasion of northern pike in the Matanuska-Susitna basin (Southcentral, Alaska, USA). Darker colors represent more species. See text for details on how vulnerability was assessed.

General Conclusions

In this study I examined the past, present, and potential future of the invasion into Southcentral Alaska by northern pike (pike; *Esox lucius*) and generated a genetic baseline for invasive pike. The genetic variability of native and invasive pike throughout Alaska was assessed using a next-generation sequencing approach, double digest restriction-site associated sequencing (ddRAD-seq). The future of the invasion, in terms of vulnerability of five Pacific salmon species (*Oncorhynchus spp.*), within the Matanuska-Susitna basin (Southcentral Alaska, USA) was assessed using a combination of intrinsic potential, connectivity estimates, and Bayesian network approaches. The vulnerability for each species was compiled and critical habitat areas, where all Pacific salmon share 'highly' vulnerable habitat, identified. The key results of these studies were:

- Throughout their native range in Alaska, pike exhibit low genetic variability compared to other freshwater fishes. The average nucleotide diversity (π) for native populations was 0.000241. The average heterozygosity was 0.0360.
- Invasive pike exhibit lower diversity than native pike. The average nucleotide diversity for introduced populations was 0.000131 and heterozygosity was 0.0227.
- Invasive pike on the Kenai Peninsula have measures of diversity between those of native populations and invasive populations in the Susitna basin and Anchorage areas.
- There was relatively high differentiation (F_{ST}) when compared to other freshwater fishes, for all populations ($F_{ST} = 0.424$), with the highest levels found between invasive groups on the Kenai Peninsula populations and Susitna basin ($F_{ST} \sim 0.668$), suggesting different founders for these two invasive groups.

- An analysis of population structure identified separation between two groups, 1) introduced populations in the Susitna basin and 2) native and Kenai Peninsula introduced populations. This further supports the idea that Kenai and Susitna populations are from different sources.
- Fine-scale structure analyses failed to detect population structure within the Susitna basin populations which indicates few founders or founding events.
- Since introduction, pike have expanded throughout the Susitna basin and I identified potential habitat that is not known to be presently occupied. This suggests that if given time and opportunity, the expansion of pike in the Matanuska-Susitna basin is likely to continue.
- Eighty-four percent of high-quality habitat potential for pike was predicted to be located in the Lower Susitna sub-basin.
- Pink salmon were found to be most vulnerable to pike with 2,458 km (15.2%) of their extent identified as highly vulnerable based on habitat overlap, and the potential for natural colonization by pike and further anthropogenic introductions.
- I found only 107 km (3.4 %) of total available high- and moderate-quality pike habitat above barriers to fish passage, suggesting that removal of existing barriers would not greatly increase potential pike habitat.
- After combining vulnerability estimates across the five Pacific salmon species, I identified 1,001 km of critical habitats where all five species were predicted to be highly vulnerable to pike.

Previous work investigating the genetic diversity of native pike, using microsatellite and allozyme markers, identified pike as a 'genetically depauperate' species (Jacobsen et al. 2005), meaning they exhibit low genetic diversity. In contrast, some populations were highly differentiated, so much so that pike were the most differentiated freshwater fishes with an F_{ST} of 0.821 (Seeb et al. 1987 for discussion see Ward et al. 1994). My work generally supports these conclusions of low diversity and relatively high divergence among some populations. I identified further reductions in genetic variability in introduced populations, which is not surprising given the nature of introductions (i.e., genetic bottlenecks). I was surprised to find that pike on the Kenai Peninsula exhibited higher genetic variability than invasive populations from the Susitna and Anchorage Areas. This result gives some credence to the idea that Kenai Peninsula populations may have come from multiple sources. That said, I was unable to determine the population affinities for any of the seven invasive populations.

Measures of genetic diversity in introduced pike indicated a bottleneck during their introduction into Southcentral Alaska. Although introduced pike were genetically poor, the lack of genetic diversity does not appear to impact their invasion success. Since introduction, pike have taken hold in the Matanuska-Susitna basin and have been expanding their range. Analyses of genetic structure identified divergence between introduced and native populations. Further analyses identified differentiation in introduced populations from the Susitna basin and Kenai Peninsula, again, suggesting different founders for the two groups. This is perhaps unsurprising, as the introduction on the Kenai Peninsula was thought to have occurred two decades after the initial introduction into the Susitna (Dunker et al. 2018).

I was able to create a genetic baseline for introduced populations in Southcentral Alaska, which can be used as a management tool. By monitoring and sampling suspected new

introductions, managers can determine whether pike came from a local or distant source. While the history of this invasion elucidates aspects like propagule pressure, methods of transport, and movement within the system, understanding the future of the invasion is also crucial.

I found that although pike are largely restricted to lower in the Matanuska-Susitna basin, due to their preference for low elevation, low gradient, and high access to floodplains, they still have large impacts on Pacific salmonids. Overall, approximately 40% of the total habitat was identified as moderate- or high-vulnerability for all Pacific salmon. Although pink salmon were the most vulnerable, life history traits like freshwater residency time was not considered but likely contributes to vulnerability. Coho salmon exhibited slightly less vulnerability than pink salmon but remain in freshwater for multiple years (Quinn 2005), presumably increasing the chance of interaction with pike. These life-history characteristics could be added my network or to future Bayesian networks, and may help to decrease the uncertainty of vulnerability estimates.

Estimates by the Alaska Department of Fish and Game for the current distribution of invasive pike do not fully overlap with predicted potential habitat. Thus, I believe the invasion is on-going and pike can continue to spread throughout the Matanuska-Susitna basin. Although little is known of pikes jumping ability, I assumed 'impassible culverts' represented barriers to upstream passage but predicted a low quantity of high- and moderate-quality pike streams (107 km) above them. Hence, it appears the removal of barriers will not allow for further colonization of otherwise naturally unreachable habitat patches. Work to restore connectivity for native salmonids by removing culverts is unlikely to come at the cost of additional invaded habitat by pike.

The availability of a reference genome allowed me to align my sequences to the reference and reduced computational requirements associated with *de novo* assembly of dd-RAD data. My

attempts at *de novo* assembly resulted in unnecessary computational efforts. If available, I strongly urge the use of a reference genome while analyzing these types of data. Further, commonly available pipelines like stacks, ipyrad, or dDocent are tremendously useful and were crucial to this study but it would be worth investigating alternative, manual pipeline approaches. Allowing the user full control of the dataset would give more clarity when issues arise and during calculations of genetic indices.

The combination of habitat suitability, connectivity, and Bayesian networks proved to be a useful tool in assessing Pacific salmon vulnerability. The ability to utilize many datatypes (i.e., quantitative, qualitative) and expand the network as new information becomes available, makes Bayesian networks a valuable tool for fisheries managers facing invasions. This is important in the case of invasions because often new data becomes available as the invasion progresses and may provide insight into the future impacts. Also, the NetMap platform worked well for assessing habitat suitability and assigning habitat metrics on the reach scale (100 m). I would recommend future researchers examining watershed habitat attributes utilize this platform. Specifically, without it, this work would not have been possible due to the lack of geospatial data on streams in Alaska.

Estimating the hydraulic distance from each 100 m reach to the nearest pike source over my entire stream network (~24,000 km) was challenging. The tools SSN and STARS were useful but calculating over a large stream network presented challenges. My approach of joining confluence-to-confluence sections of river then back calculating the distance from the midpoint of those to the midpoint of each 100 m reach contained within was very involved (> 30 steps) and investigating alternate methods for these calculations is recommended. One idea would be to break the stream network into multiple sections, similar to my seven sub-basins, and calculate

the distance from each source to the end of the sub-basin. Next, assign this value to the starting point of the next, connected, sub-basin and calculate the distance to all reaches within. Finally, adding previous values to the new sub-basin would give the distance to the nearest pike source.

Future genetic research should aim to expand the search for potential founder populations within Alaska. Currently my study is limited to three native sources and would benefit greatly from expanded sampling to create a statewide genetic baseline. This is particularly true in light of the differences highlighted between the two invasive groups. Also, suspected founder populations were included in these analyses, yet there was high differentiation between invasive and all native populations, as well as little evidence of admixture. Finally, expanding the analyses to include North American populations from outside of Alaska will help to elucidate the broader question of pike refugia during the Pleistocene. Some hypothesize that present day Alaska was a refuge and/or bridge that acted as a source for North American populations. Currently, I am working to incorporate a second genetic dataset which includes native populations from Alaska and elsewhere in North America along with more invasive populations from Southcentral Alaska. I am also investigating the post-glacial relict status of pike from Yakutat, Alaska. I believe my use of next-generation sequencing, and inclusion of more populations, could inform some of the questions posed above.

Other future work should include ground-truthing of the pike intrinsic potential model. My model was created in an area of limited pike distribution data so 'truthing' was carried out across a small dataset. However, all known pike points fell within my high-quality habitat class, so I am confident in the model. Also, since a true sockeye salmon intrinsic potential model is does not exist, the creation would benefit this study and future habitat modeling efforts. As most sockeye salmon rear in lakes, the development of a 'lake-type' model that predicts habitat

potential for lakes across the stream network, would be greatly beneficial. A river-type sockeye IP would also be beneficial and provide more robust predictions of sockeye vulnerability than those presented here. Finally, research techniques like radio telemetry could be used to investigate the duration in which pike journey into sub-optimal habitat for feeding. It is unknown if or for how long pike will 'follow' out-migrating smolt into large rivers, otherwise unused by pike. If it is determined that pike follow out-migrating smolt, then my Bayesian network could be modified to incorporate this window of the salmon life cycle.

In summary, the research described here contributes to the breadth of knowledge about invasion biology and genetics as well as the vulnerability of native fishes to an invasive top predator. It adds a genetic baseline for invasive pike in Southcentral Alaska and I have provided a framework for fisheries managers to triage large landscapes, such as the Matanuska-Susitna basin, and identify critical habitat areas in which invasive species management actions will have the greatest impacts on Pacific salmon. Further, by providing baseline data necessary to examine the evolutionary potential of pike, thresholds can be identified, and knowledge gained into how little genetic variation top predators can maintain yet still become a potent invader. Although it is unclear whether introduced pike populations have locally adapted to the conditions in their new areas, my finding suggests that genetic diversity is not a requisite condition of successful invasion. For now, pike are continuing to expand to available habitat in the Matanuska-Susitna basin, despite the apparent lack of genetic diversity, and will likely continue to impact already declining Pacific salmon populations.

References

Dunker, K. J., A. J. Sepulveda, R. L. Massengill, and D. S. Rutz. 2018. The northern pike, a prized native but disastrous invasive. Pages 356–398 *in* C. Skov and P. A. Nilsson, editors. Biology and Ecology of Pike, 1st edition. CRC Press, Boca Raton.

Jacobsen, B. H., M. M. Hansen, and V. Loeschcke. 2004. Microsatellite DNA analysis of northern pike (*Esox lucius* L.) populations: insights into the genetic structure and demographic history of a genetically depauperate species. Biological Journal of the Linnean Society 84(1):91–101.

Quinn, T. P. 2005. Downstream migration: to sea or not to sea? Pages 209–228 The behavior and ecology of Pacific salmon and trout, 1st edition. University of Washington Press, Vancouver.

Seeb, J. E., L. W. Seeb, D. W. Oates, and F. M. Utter. 1987. Genetic variation and postglacial dispersal of populations of northern pike (*Esox lucius*) in North America. Canadian Journal of Fisheries and Aquatic Sciences 44(3):556–561.

Ward, R. D., M. Woodwark, and D. O. F. Skibinski. 1994. A comparison of genetic diversity levels in marine, freshwater, and anadromous fishes. Journal of Fish Biology 44(2):213–232.

Appendix

Appendix A. 2017 University of Alaska Fairbanks Institute for Animal Care and Control approval.

(907) 474-7800
(907) 474-5993 fax
uaf-iacuc@alaska.edu
www.uaf.edu/iacuc

Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

May 17, 2017

To:	Peter Westley Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[921163-3] Rapid adaptation and the biological invasion of northern pike to Southcentral Alaska

The IACUC reviewed and approved the Revision referenced above by Designated Member Review.

Received:	May 9, 2017
Approval Date:	May 16, 2017
Initial Approval Date:	May 16, 2017
Expiration Date:	May 16, 2018

This action is included on the May 11, 2017 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

Appendix B. 2017 State of Alaska Department of Fish and Game Fish Resource Permit.

STATE OF ALASKA
DEPARTMENT OF FISH AND GAME
333 Raspberry Road
ANCHORAGE, ALASKA 99518

Permit No. **SF2017-168**

Expires: **12/31/2017**

FISH RESOURCE PERMIT
(For Scientific/Collection Purposes)

This permit authorizes: **Peter Westley**
(whose signature is required on page 3 for permit validation)
Of
University of Alaska Fairbanks – College of Fisheries and Ocean Sciences
PO Box 757220, Fairbanks, AK 99775
(907) 474-7458 **pwestley@alaska.edu**

to conduct the following activities from **June 1, 2017** to **December 31, 2017** in accordance with AS 16.05.930 and AS 16.05.340(b).

Purpose: To quantify whether anti-predator behaviors are greater in juvenile salmon populations with histories of exposure to highly predatory northern pike compared to populations that have less time of exposure.

Location: Deshka River (247-41-10200-2081), Cottonwood Creek (247-50-10300), Caswell Creek (247-41-10200-2190), Montana Creek (247-41-10200-2250), Fish Creek (247-50-10330), Trapper Creek (247-41-10200-2341), Chena River (334-40-11000-2490-3301), Delta Clearwater River (334-40-11000-2490-3416), Salcha River (334-40-11000-2490-3329), Chatanika River (334-40-11000-2490-3151-4020), Ruth Burnett and William Jack Hernandez Sport Fish Hatcheries

Species: Chinook and coho salmon, other species incidentally

Method of Capture: Fyke/hoop net **(see Stipulation #6 for exception)**, minnow trap, stick seine, hatchery transfer **(see Stipulations #7–10)**

Final Disposition: ≤400 juveniles of each Chinook and coho salmon may be captured and temporarily held for anti-predator behavior assessment. Fish may be individually transferred to a streamside aquarium for behavioral testing and observation, which should not exceed 30 minutes. Following assessment, fish may be measured, scale sampled, marked with a small caudal fin clip, and then released alive back into capture site waters **(see Stipulations #11–13)**. While awaiting assessment, fish may be held in a flow-through container in the capture site waters for ≤6 hours.
All unintended mortalities must be recorded and returned to capture site waters.
All non-target species captured should be recorded and immediately released back into capture site waters.

COLLECTION REPORT DUE January 31, 2018 and **RESEARCH REPORT DUE June 30, 2018**; see **Stipulations #2** and **#3** for more information. Data from such reports are considered public information. Reports must be submitted by email (dfg.dsf.permitcoordinator@alaska.gov) or by mail to: Alaska Department of Fish and Game, Division of Sport Fish-HQ, 333 Raspberry Rd, Anchorage, AK 99518. A report is required whether or not collecting activities were undertaken.

GENERAL CONDITIONS, EXCEPTIONS, AND RESTRICTIONS

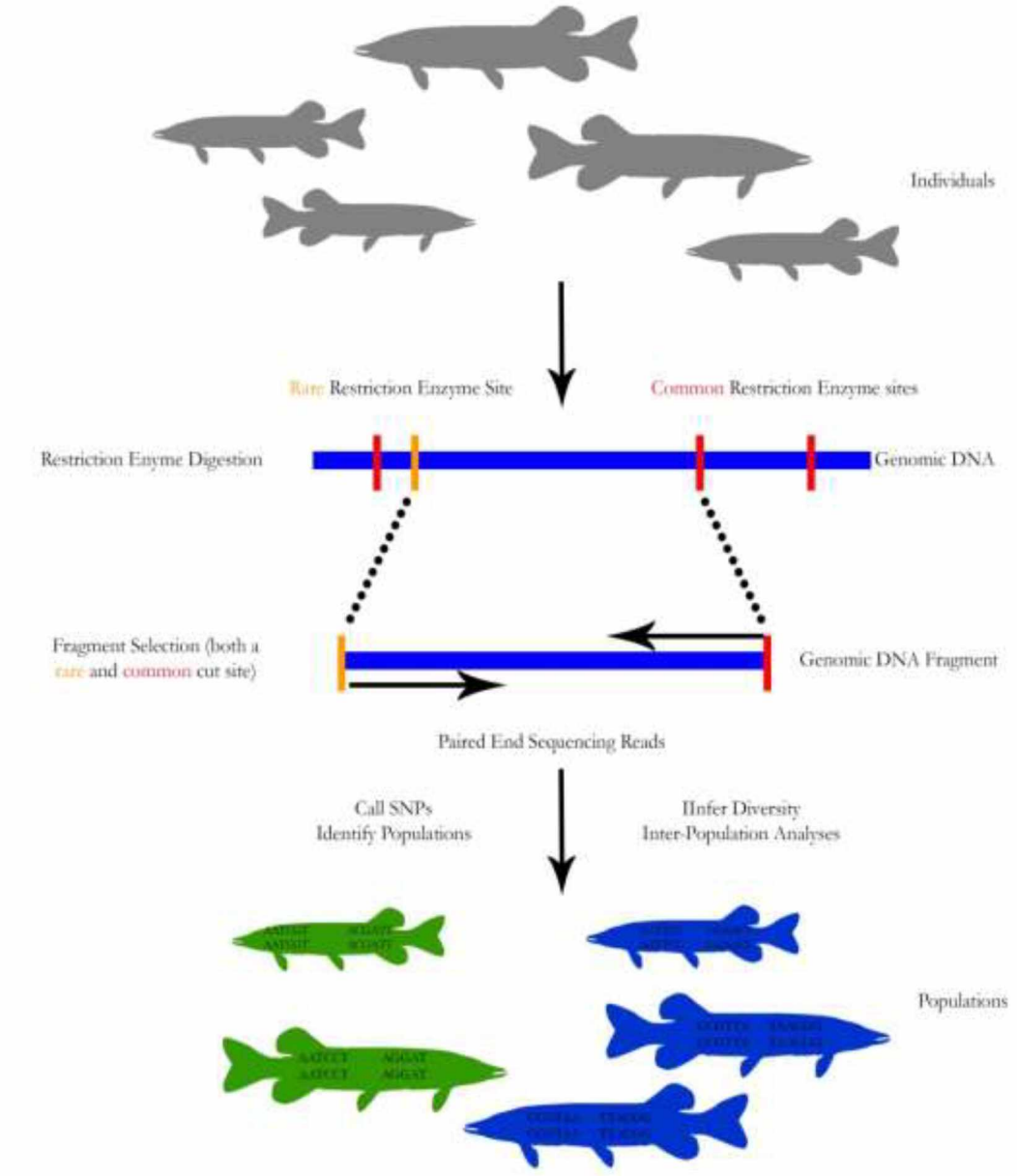
1. This permit must be carried by person(s) specified during approved activities who shall show it on request to persons authorized to enforce Alaska's fish and game laws. This permit is nontransferable and will be revoked or renewal denied by the Commissioner of Fish and Game if the permittee violates any of its conditions, exceptions, or restrictions. No redelegation of authority may be allowed under this permit unless specifically noted.
2. No specimens taken under authority hereof may be sold, bartered, or consumed. All specimens must be deposited in a public museum or a public scientific or educational institution unless otherwise stated herein. Subpermittees shall not retain possession of live animals or other specimens.
3. The permittee shall keep records of all activities conducted under authority of this permit, available for inspection at all reasonable hours upon request of any authorized state enforcement officer.
4. Permits will not be renewed until detailed reports, as specified in the Stipulations section, have been received by the department.
5. UNLESS SPECIFICALLY STATED HEREIN, this permit does not authorize the exportation of specimens or the taking of specimens outside of existing regulations.

Permit Coordinator
Division of Sport Fish

T. Taube for
Director
Division of Sport Fish

5-31-17
Date

Appendix C. Process of ddRAD-sequencing. Genomic DNA from individuals is extracted using restriction enzymes which digest specific sized target sequences. Genomic fragments containing rare and a common cut size are sequenced in the forward and backward directions. SNPs are discovered, and populations inferred.



Appendix D. Attributes that have been deemed important predictors of northern pike in their native range.

Attribute	Source	Units	Description	References
Watershed area	NetMap Reach	km^2	The total area of watershed located above a reach.	R. Shaftel, unpublished
Stream order	NetMap Reach	Classes, 1^{st} - 10^{th}	Strahler method (1957) for calculating stream order.	R. Shaftel, unpublished
Stream elevation	NetMap Reach	m	The reach elevation.	R. Shaftel, unpublished; Spens et al. 2007
Watershed lake density	DEM	%	The percentage of lakes and ponds within a watershed.	R. Shaftel, unpublished; Spens et al. 2007
Floodplain presence	NetMap Reach	Yes or No	The extent of floodplain is calculated from bankfull depth.	R. Shaftel, unpublished
Distance to invaded lake	DEM	m/km	The distance of a reach from a known pike presence lake.	Spens et al. 2007

Lake inlet and outlet	DEM	Yes or No	The presence of an outlet and inlet in invaded lakes.	Spens et al. 2007
Maximum Downstream Gradient	NetMap	Unitless (m/m)	The maximum slope downstream of a reach.	R. Shaftel, unpublished; Spens et al. 2007
Vegetation Density	--	Plant/m^2	The amount of vegetation available in the system.	Casselman 1996
Connecting waterways	DEM	--	Description of connectivity of the system.	Casselman 1996, Spens et al. 2007
Channel Depth	NetMap	m	The water level in the system.	Casselman 1996